ARTICULATED ACANTHODIAN FISHES FROM THE OLD RED SANDSTONE OF ENGLAND, WITH A REVIEW OF THE STRUCTURE AND EVOLUTION OF THE ACANTHODIAN SHOULDER-GIRDLE

BY

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Pp. 111-213; 21 *Plates,* 43 *Text-figures*

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CONTENTS

SYNOPSIS

Three species of acanthodians are described from the Ditton Series of Wayne Herbert quarry, SW Herefordshire: the climatiids *Ptomacanthus anglicus* gen. et sp. nov. and *Vernicomacanthus waynensis* gen. et sp. nov., and the ischnacanthid *Uraniacanthus spinosus* gen. et sp. nov. *Climatius uncinatus* Powrie from the Lower Old Red Sandstone of Scotland is made the type of *Vernicomacanthus* gen. nov. The relationships of these species are briefly discussed, and some comments are made on the regional variation in the squamation and the nature of the dentition, particularly in connexion with *P. anglicus*. The head skeleton of *Climatius reticulatus* Agassiz is redescribed to provide a standard of comparison for *P. anglicus*, and Watson's interpretation of the gill-covers is contested.

The shoulder-girdle is described in a range of species covering all families of acanthodians, and where possible the pectoral fin is also described. It is confirmed that the acanthodiforms and ischnacanthiforms lack dermal plates, and in these groups the shoulder-girdle comprises only endoskeletal structures. Advanced forms exhibit a procoracoid separate from the scapulocoracoid, and this condition may be associated with the possession of a mobile pectoral spine. The climatiiforms have both ventral plates and prepectoral-intermediate spines associated with the scapulocoracoid, in addition to the pectoral spine. Primitively the plates form a paired lateral and a median series, and all but the posterior median plate (posterior lorical) are associated with a spine of the prepectoral-intermediate series.

Descriptions are given of the climatiids *Erriwacanthus manbrookensis* sp. nov. from the Downton Series of Worcestershire; *Ptomacanthus* sp. indet 1 from the Ditton Series of Herefordshire; and *Ptomacanthus* sp. indet. 2 from the Dittonian of the Ukraine. *Onchus arcuatus* Agassiz is referred to *Sabrinacanthus* gen. nov., and new shoulder-girdle material of this species is described from the Ditton Series of Gloucester. The Gyracanthidae are re-evaluated and referred to the Climatioidei; they include *Gyracanthus* (the type genus), *Gyracanthides* and *Oracanthus*. *Rhadinacanthus* (Diplacanthidae) is considered to be a valid genus.

The homologies, significance and evolution of the dermal elements in the climatioid shoulder-girdle are discussed. The spines and plates are reduced in divers ways, and a marked contrast in this regard is found between climatioids and diplacanthoids. The evolutionary tendencies in acanthodiforms are related to the development of a mobile pectoral spine, as may also be the case in climatioids. The acanthodiforms and ischnacanthiforms may be more closely related to each other than either group is to the climatiiforms. The scapulocoracoid of acanthodians approaches closely the primitive gnathostome type, and is distinct from that of placoderms. In acanthodiforms, although the scapulocoracoid becomes specialised in relation to the development of a mobile fin-spine, it can still be compared closely with that of primitive actinopterygians. The ventral plates of climatiiforms are not homologous with those of osteichthyans or placoderms. The pectoral fin and its articulation with the girdle may indicate that acanthodians are phylogenetically closer to osteichthyans than they are to chondrichthyans, but the shoulder-girdle yields no decisive evidence on the relationships of acanthodians.

I. INTRODUCTION

THE articulated acanthodians described below were collected by Dr E. I. White and Mr H. A. Toombs in August 1934. The specimens were obtained from the siltstone lenticle that yielded White's (1935) complete specimens of *Pteraspis rostrata* (Agassiz). They have been mentioned in a number of publications (e.g. White 1935 : 383, 1950 : 56; Denison 1956 : 394, 425; Allen & Tarlo 1963 : 145–146), but they have not been described and have unfortunately attracted some misleading taxonomic designations. They are, however, well worthy of description, both for the rarity of articulated acanthodians in Devonian rocks and for their unusually fine preservation. Together with the species from Angus, Scotland, they are the only articulated Lower Devonian acanthodians, and the oldest intact specimens.

The occurrence of the Wayne Herbert fauna has been described by White (1935 : 383). There is general agreement that it comprises fluvial species, trapped by the drying up of the body of water in which they lived.

The specimens have been prepared by etching away the bone with diluted hydrochloric acid, and the resulting moulds have been studied with the aid of rubber casts. The illustration of acanthodians, particularly primitive species in which there are many small bones in the head, has always been difficult. In an effort to maintain a distinction between the specimens (i.e. the evidence) and my interpretations of them, I have attempted in the first part of this paper to illustrate the descriptions mostly with large photographs, accompanied in some cases by key drawings in the text, and then quite separately to summarise the results in restorations. I have selected the shoulder-girdle for special study in the second part of this paper, because it is the only structure found throughout the group in a wide range of species, apart from scales and spines, and thus the only structure likely to throw much light on acanthodian interrelationships. This is not, however, an exhaustive account, and only forms that seemed likely to yield useful results have been studied; no species that deviates markedly from the 'normal' pattern in its family has been deliberately ignored. I believe that a sufficiently wide range of forms has been studied to allow some general conclusions to be drawn. The pectoral fin is less frequently preserved, but where possible it has also been studied.

The following classification is used:

Order ACANTHODIFORMES
  Family **ACANTHODIDAE**; *Acanthodes*
  Family **CHEIRACANTHIDAE**; *Cheiracanthus*
  Family **MESACANTHIDAE**; *Mesacanthus*

Order ISCHNACANTHIFORMES
  Family **ISCHNACANTHIDAE**; *Ischnacanthus*, *Uraniacanthus* gen. nov.

Order CLIMATIIFORMES
  Suborder CLIMATIOIDEI
    Family **CLIMATIIDAE**; *Brachyacanthus*, *Climatius*, *Erriwacanthus*, *Parexus*, *Ptomacanthus* gen. nov., *Sabrinacanthus* gen. nov., *Vernicomacanthus* gen. nov.
    Family **EUTHACANTHIDAE**; *Euthacanthus*
    Family **GYRACANTHIDAE**; *Gyracanthus*, *Gyracanthides*, *Oracanthus*
  Suborder DIPLACANTHOIDEI
    Family **DIPLACANTHIDAE**; *Diplacanthus*, *Rhadinacanthus*

Throughout this paper the endoskeletal bones are described as though they are solid structures, although they comprise perichondral bone around a space, originally filled with cartilage and now frequently containing calcite. This infilling is of little interest in the present connexion, and in several species has been adequately described by earlier workers.

Finally the evolution of the shoulder-girdle and the relations of acanthodians are discussed. The main results relate to general evolutionary trends and the interrelations of climatiiforms, but some aspects of the interrelations of the three orders of acanthodians, and the relationships of acanthodians with chondrichthyans and osteichthyans are also considered.

For the loan of specimens I am indebted to Drs S. M. Andrews and C. D. Waterston, Royal Scottish Museum; Dr H. Jaeger, Humboldt University, Berlin; Dr T. Ørvig, Swedish Museum of Natural History; Mr J. M. Edmonds, University Museum, Oxford; and the authorities of the Scottish and London offices of the Institute of Geological Sciences. Miss V. T. Young has assisted estimably with the illustrations, and Drs S. M. Andrews and C. Patterson have kindly read and commented on the manuscript.

The following abbreviations are used: BM, British Museum (Natural History); GSE, Institute of Geological Sciences, Edinburgh; GSM, Institute of Geological Sciences, London; HU, Palaeontological Institute of the Humboldt University, Berlin; RSM, Royal Scottish Museum; SMNH, Swedish Museum of Natural History; UMO, University Museum, Oxford.

II. THE WAYNE HERBERT ACANTHODIANS

Order CLIMATIIFORMES
Suborder CLIMATIOIDEI
Family **CLIMATIIDAE**

PTOMACANTHUS gen. nov.

Etymology. Gr. *ptoma*, a corpse; Gr. *akantha*, a thorn.

Definition. Acanthodians with coarsely-ribbed spines; the shoulder-girdle is perichondrally ossified with a broad scapular blade and large coracoid process, and carries paired prepectoral spines 1 and 3; there is a median prepectoral spine; the anterior dorsal fin-spine is curved and not much longer than the posterior, which is almost straight; the body scales each have a moderately high crown with a posterior point and a paired lateral point; the dentition comprises both upper and lower jaw teeth in the form of spirals with several flat, blade-like cusps; there are no dentigerous jaw-bones.

Type species. *Ptomacanthus anglicus* sp. nov.

Remarks. The terms given to the prepectoral spines are explained in the second part of this paper.

PTOMACANTHUS ANGLICUS sp. nov.

Pl. 1, fig. 2, Pls. 4–6

1950 large Brachyacanthids; White : 56
1961 a large acanthodian; Denison : 181

Etymology. From Angle, a member of the Teutonic tribe that settled in England in the 5th Cent A.D.

Definition. A species reaching a length of at least 300 mm; with three pairs of intermediate spines posterior to the shoulder-girdle. This is the only definable species.

Type. The holotype is a complete fish in part and counterpart, BM P.19998–9 (Pl. 1, fig. 2).

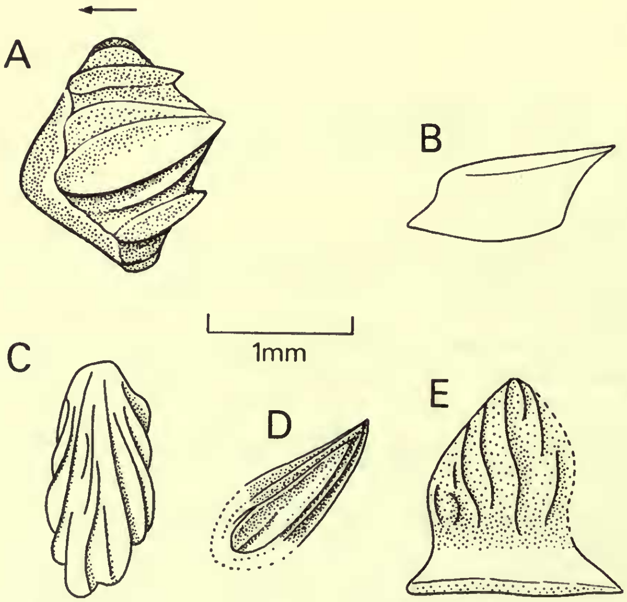
Horizon. Ditton Series, about 66 m above the main '*Psammosteus*' Limestone, in the *Pteraspis crouchi* zone.

Locality. Wayne Herbert quarry, near Newton, SW. Herefordshire; in the siltstone lenticle described by White (1935 : 383).

Material. This study is based on six individuals in the BM; P.19998–9, the holotype; P.16615, a large area of squamation from the middle of the body, from which thin sections of the scales have at some time been prepared; P.20002–3, an almost complete fish in part and counterpart but not showing the head and caudal fin well; P.24919a, b, a skull in part and counterpart; P.53037–8, the posterior part of the body as far as the root of the tail, in part and counterpart; P.53285a, b, the left pectoral spine and part of the scapulocoracoid. The thin sections in the collection do not show fine details of structure, and bone histology is not included in this study.

REMARKS. Shoulder-girdles and spines of *Ptomacanthus* are found at other horizons in the English Dittonian and probably belong to a distinct species. They are described in the second part of this paper, together with a shoulder-girdle of *Ptomacanthus* sp. from the Ukraine (pp. 175–176). New species are not named for these specimens as it is impossible to provide satisfactory definitions.

DESCRIPTION. (i) *General features*. *P. anglicus* is a large climatiid with a moderately deep body clothed in thick scales, and with thick tesserae on the skull. The length of the holotype is estimated to be 325 mm. Additional measurements are given in Table 1. The holotype and other articulated specimens are laterally compressed, but in P.20002–3 the ventral region of the shoulder-girdle and the body wall between the intermediate spines have been turned in the same plane as the flank. This suggests a moderately deep body with a broad venter. The detached head, P.24919a, b, is dorsoventrally compressed and this indicates that the skull-



TEXT-FIG. 1. *Ptomacanthus anglicus* gen. et sp. nov. Lower Old Red Sandstone. A, crown of dorsal flank scale; B, side profile of flank scale; C, crown of scale from lateral surface of scapular blade; D, crown of scale from web of posterior dorsal fin; E, lateral view of scale from ventral surface of shoulder-girdle. A, B, D after holotype, BM P.19998–9; C, E after BM P.20003. Ditton series, Wayne Herbert quarry, Newton, Herefordshire, England.

Table 1

Length (in millimetres) of exserted portion of fin-spines of *Ptomacanthus anglicus* gen. et sp. nov. measured in a straight line from the middle of the base line to the tip.

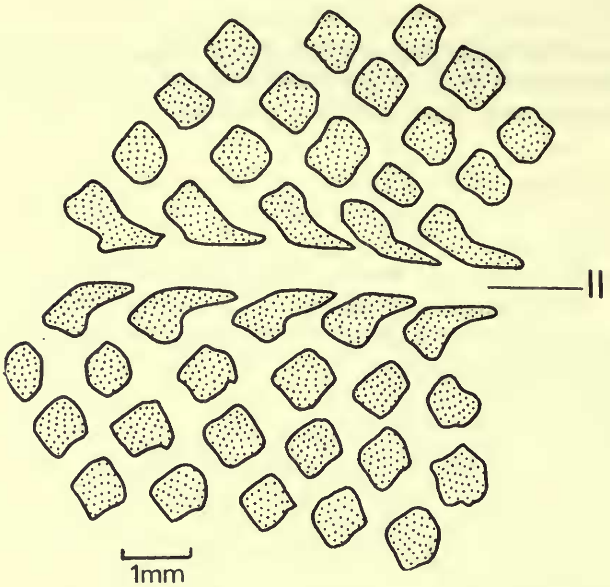
Specimen	Ant. dorsal	Post. dorsal	Pectoral	Pelvic	Anal
P.19998–9	40	35	—	Ca. 24	38
P.20002–3	30	28	Ca. 35	20	Ca. 28
P.53037–8	—	—	—	—	41
P.53285a, b	—	—	Ca. 50	—	—

roof was broad. The eyes were large, as in other acanthodians, and the snout is short and blunt. The fin-spines are placed much as they are in *Climatius reticulatus* Agassiz, with the anterior dorsal inserted posterior to the base of the pectoral and the posterior dorsal situated between the transverse levels of the pelvics and anal. None of the spines is unduly lengthened.

(ii) *Squamation.* The scales of the flank are of a uniform basic type. They have a moderately high crown, which is terraced at either side of a navicular central area which projects posteriorly to a distinct point (Text-fig. 1A). A lateral navicular area may also project back to a posterior point at either side of the central area. Generally the central area is slightly depressed, but it may be flat, and in some cases it bears a slight median ridge. The development of the lateral posterior points also varies, but apparently in a random way over the flank. In some scales they are prominently formed and in others barely distinguishable. Dorsally on the flank the crowns are directed posterodorsally, but lower down their orientation gradually changes so that at the level of the horizontal septum they are horizontally placed, and in the lower part of the flank they become posteroventrally directed. Over most of the body the scales are of almost uniform size, with, e.g., the length of the crown rarely much above 1 mm in the holotype; but they are enlarged ventrally behind the shoulder-girdle in the body cavity region, and in the holotype the crowns here reach a length of about 2 mm. The bases of the scales are slightly swollen (Text-fig. 1B), and in ventral view show typical concentric growth lines. At either side of the main lateral-line the bases of the scales are drawn out to border the course of the line (Text-fig. 2), but on present evidence it is not possible to say whether they are extended in the anterior or posterior direction.

A distinctive type of scale is found in the shoulder-girdle region. On the lateral face of the scapular blade, to which the scale bases are closely applied, the crowns are broad and flat, and ornamented with narrow ridges (Text-fig. 1C). It appears that the terracing of the scales has been destroyed by their flattening, in comparison with normal flank scales. In contrast to this, on the ventral surface below the coracoid and coracoid process, the scales crowns are high and laterally compressed, although again they are ornamented with narrow ridges and have a thin, flat base (Text-fig. 1E).

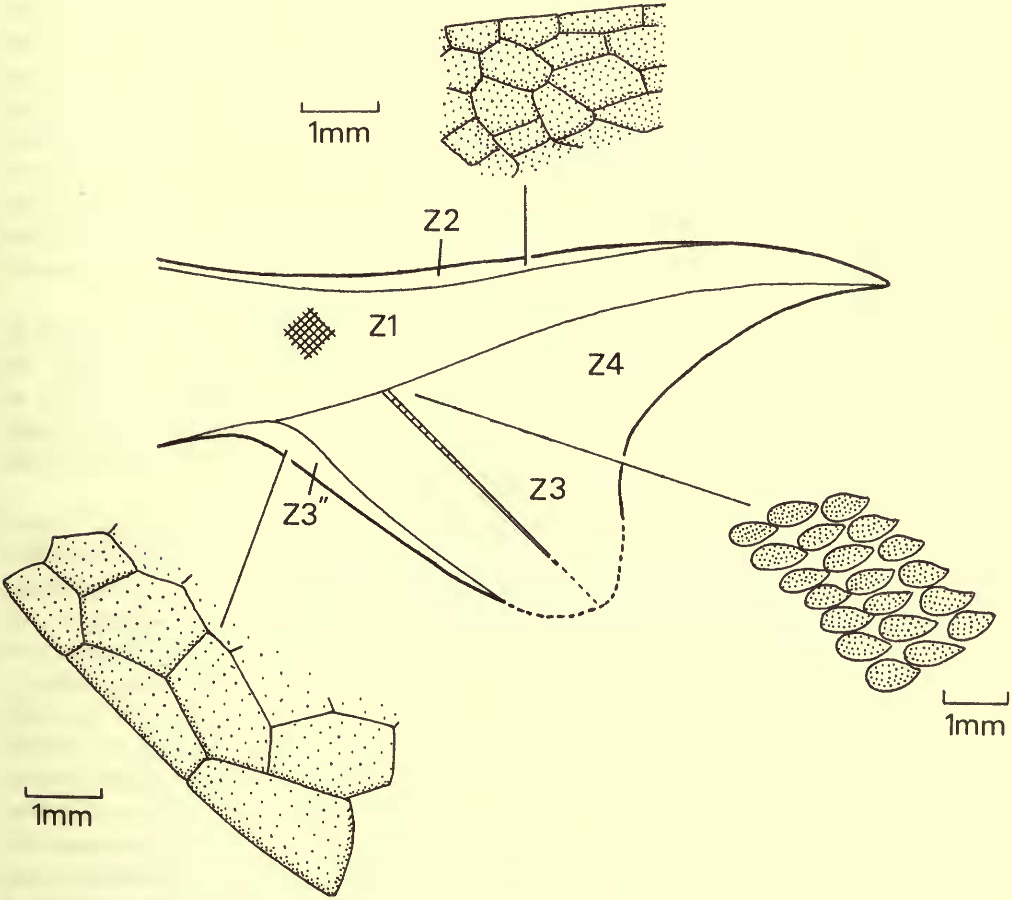
The scales on the webs of the dorsal and anal fins are fundamentally the same as the flank scales. The central navicular area is, however, long and narrow, and there are no lateral areas or lateral points (Text-fig. 1D). As in other acanthodians, the fin scales are arranged in long, straight rows.



Text-fig. 2. *Ptomacanthus anglicus* gen. et sp. nov. Lower Old Red Sandstone. Flank scales bordering the main lateral-line. BM P.16615. Ditton series, Wayne Herbert quarry, Newton, Herefordshire, England.

The squamation of the tail can be compared with that of *Acanthodes*, in which four scale zones have been described (Heyler 1969, Miles 1970). Zone 1 (*Z1*, Text-fig. 3) comprises normal body scales, situated on the caudal prolongation; they require no comment. Zone 2 (*Z2*) lies in an epichordal position, and in *Acanthodes* it comprised regular rows of scales set almost at right angles to the caudal prolongation, but with a differentiated outer region of smaller scales more posteriorly orientated (zone 2″). The scales of zone 2 are, however, not differentiated in this way in *P. anglicus*. Instead they form a mosaic of unornamented, thick scales, in which the basic regular arrangement has been lost. There is no sign of an axial caudal lobe, but a hypochordal lobe with distinct ventral and longitudinal divisions can plainly be seen. The scales of these divisions have been described as zones 3 and 4 (*Z3*, *Z4*) in *Acanthodes*, but there are no important differences between the scales of these divisions in *P. anglicus*. The scales are arranged in long rows, and become progressively finer distally. They have slightly depressed navicular crowns without ornamentation, which are arranged at right angles to the long axes of the rows. The most distal regions of the hypochordal lobe, with very fine scales, cannot be observed clearly, but it is likely that there is some branching of the scale rows here as in other acanthodians (Miles 1970 : 355). Anteriorly at the root of the ventral division of the hypochordal lobe, the scales are enlarged and somewhat irregularly arranged, as in zone 2. I propose to distinguish this region as zone 3″. An exactly comparable zone has been described in *Parexus falcatus* Powrie by Dean (1907 : 215, Text-fig. 20), and I have recorded a similar condition in *Ischnacanthus gracilis* (Egerton) and *Mesacanthus mitchelli* (Egerton) (Miles 1970 : 356) and briefly noted its functional significance.

If one excludes the tesserae of the head (*v. infra*) and the fin scales, there is remarkably little regional differentiation of the squamation in *P. anglicus*. The only notable variation from the standard type of (flank) scale occurs in the shoulder region, with flat lateral and blade-like ventral scales. This is in marked contrast to conditions in some sharks, e.g. *Heterodontus francisci* (Girard) (Daniel 1914), in which there are distinct dorsal and ventral scales with variously modified types of each. One type of dorsal scale occurs at the base of the pelvic fin and posterior to



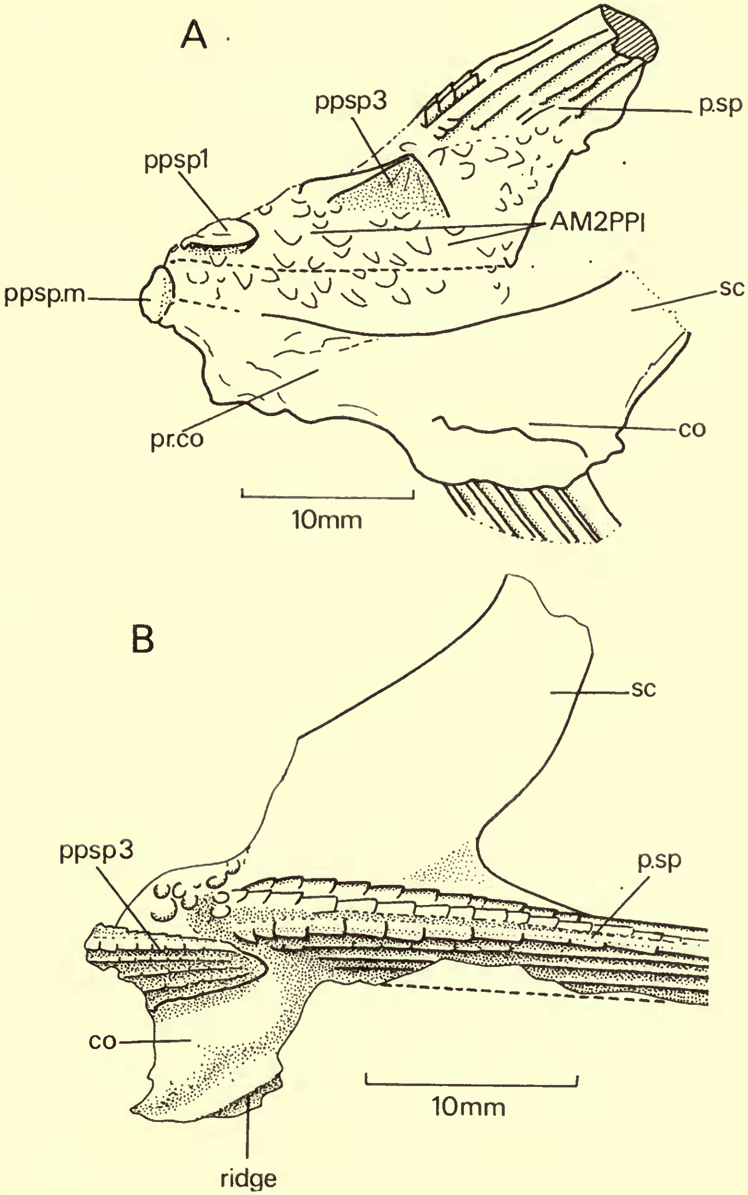
Text-fig. 3. *Ptomacanthus anglicus* gen. et sp. nov. Lower Old Red Sandstone. Regional differentiation of squamation on caudal fin. After holotype, BM P.19998–9 and BM P.53037. Ditton Series, Wayne Herbert quarry, Newton, Herefordshire, England.

the cloaca ('anchor scales'). Although the venter is well seen in one specimen of *P. anglicus* (BM P.20003), there is no indication of modified scales which might have been situated near the vent.

(iii) *Spines.* These are seen in the illustrations and may be described briefly. The prepectoral spines are noted below with the shoulder-girdle. The pectoral spine is not completely preserved, but is known to be moderately curved and ornamented on both its dorsal and ventral surface with six or seven ribs. These ribs bear nodes which are especially prominent proximally; they are of the familiar cone-like climatioid type with each node appearing to fit into the adjacent proximal node. The pelvic spine is also gently arched, and is ornamented with three ribs on both its dorsal and ventral surface. The anterior dorsal fin-spine resembles the pectoral in its size and curvature. It differs, however, in lacking nodes on the surface ribbing, except on the anterior margin. There are three or four ribs at either side. The posterior dorsal fin-spine is slightly shorter than the anterior and is almost straight, so that the two spines are distinct. Like the anterior spine, it is ornamented with three or four smooth ribs at each side, but in both cases imperfect preservation makes it difficult to be sure of the number. The anal fin-spine is slightly curved and bears five smooth ribs at each side. The intermediate spines are poorly seen in the holotype (Pl. 1, fig. 2) and in BM P.20003. There is no firm evidence of more than three (*v. infra*), of which the most anterior is situated some distance behind the shoulder-girdle. The first is the shortest and the last the longest, as is usual in climatioids, and all are ornamented with slender ribs.

(iv) *Shoulder-girdle.* In BM P.20003 the left side of the shoulder-girdle is seen in ventral view, and the right scapulocoracoid is seen in mesial aspect. Text-fig. 4A is a sketch of this specimen which may be used as a key diagram for Pl. 4, fig. 2. Text-fig. 4B is a drawing of a cast made from BM P.53285a, b, used as a two-piece mould; it shows much of the left shoulder-girdle in lateral aspect. Our knowledge is derived from these two specimens.

The scapulocoracoid has a broad scapular blade (*sc*) and deep coracoid region (*co*). The full height of the blade is not preserved, but it was presumably considerable. There is a long coracoid process (*pr.co*). More details of the scapulocoracoid may be obtained from other specimens of *Ptomacanthus* (p. 175), making it unnecessary to extend this account of *P. anglicus.* In front of the pectoral spine there are two lateral prepectoral spines (*ppsp 1*, *ppsp 3*; see p. 162*f* for terminology). The area mesial to these spines, under the coracoid process, is covered by the high crowned scales described above. Although the true conditions cannot be clearly seen in P.20003, evidence from *Climatius reticulatus* suggests that the pectoral spine, prepectoral spines and scales are attached to one or more thin, lateral dermal plates with ventral and ascending laminae, which are attached to the surface of the scapulocoracoid at a deep level in the corium (see pinnal plates, p. 163). Whether there were two median dermal plates as in *Climatius* is not clear, but there is evidently a median prepectoral spine (*ppsp.m*) which may have been attached to a small anterior plate (cf. anterior lorical, p. 163). The coracoid of P.53285 bears a low ridge (*ridge*, Text-fig. 4B) in the position of the first intermediate spine of *Climatius* and other



Text-fig. 4. *Ptomacanthus anglicus* gen. et sp. nov. Lower Old Red Sandstone. A, shoulder-girdle; key-diagram for Pl. 4, fig. 2. BM P.20003. B, shoulder-girdle in lateral view, from a cast. BM P.53285a, b. Ditton series, Wayne Herbert quarry, Newton, Herefordshire, England.

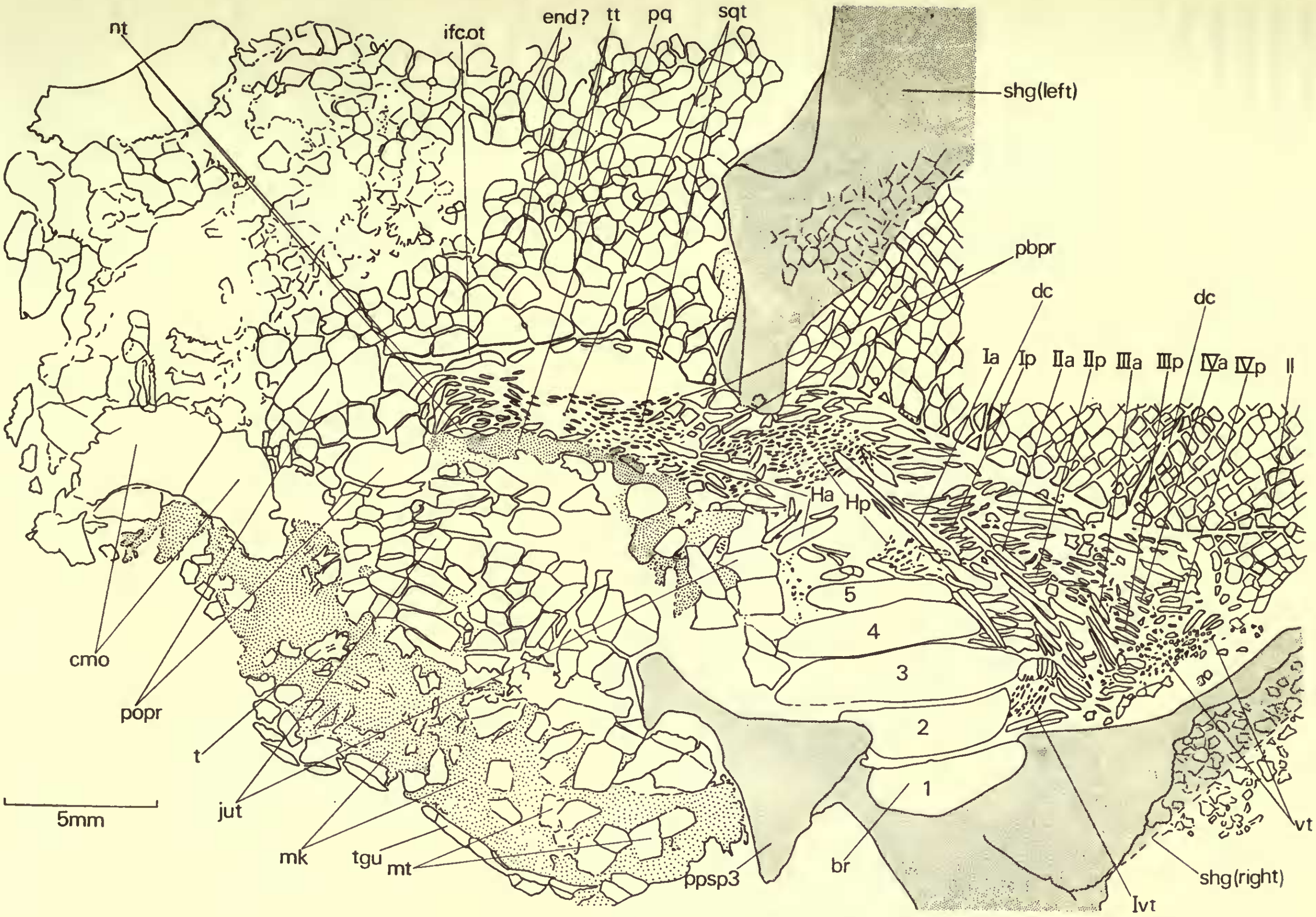
genera (p. 165), which is attached to the shoulder-girdle. P.20003, however, provides no supporting evidence of a ventrally directed spine in this position, and I provisionally conclude that it was absent. Further material may modify this view.

(v) *Gut contents*. The holotype (BM P.19998–9) had a head-shield of *Cephalaspis* sp. within the little-disturbed squamation of the posterior region of the visceral cavity. The animal appears to have been swallowed whole, head first, in the way that prey are ingested by many modern fishes. Denison (1956 : 426) records: 'That this *Cephalaspis* had actually been eaten is supported by the fact that it is the only small individual and the only non-articulated specimen of this genus in the lenticle, and also by the poor preservation of its surface, which suggests that it had been acted on by digestive juices.' The bone tissue of the specimen has been completely removed during preparation, but the *Cephalaspis* is clearly seen as an impression and in casts (Pl. 1, fig. 2). The tail of the *Cephalaspis* appears to have been disarticulated, but the squamation of the acanthodian is destroyed in this region.

(vi) *Head of Climatius reticulatus*. Although the head of *P. anglicus* shows some details of structure more clearly than any previously described climatiid, notably of the dentition and lower jaw, the whole structure can be described most satisfactorily by comparison with *C. reticulatus*.

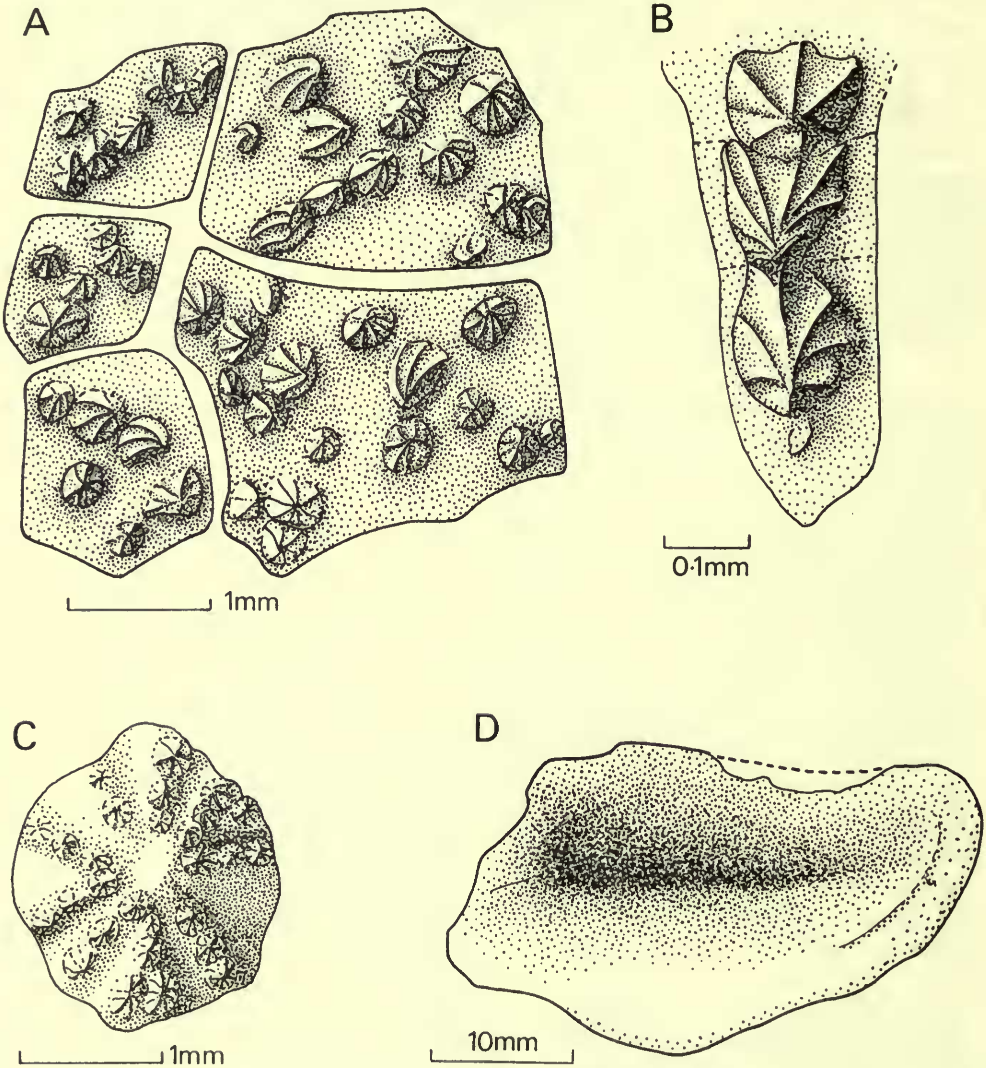
Shortly after I commenced the study of acanthodians in Stockholm in 1964, it became apparent that Watson's (1937) account of the dermal head skeleton in *C. reticulatus* does not always correspond with the structures shown by the specimens in his photographs. This is important because Watson's interpretations of other acanthodians are founded on *C. reticulatus*, and his restorations are used as evidence for his Aphetohyoid hypothesis. However, at that time the specimens available did not permit me to come to a satisfactory new interpretation, and the specimen I figured has since proved in some respects to be seriously misleading (Miles 1966 : 169, Text-fig. 9). Subsequently I continued to study *Climatius* in the Royal Scottish Museum (1964–1968), and I have now completed this work in the British Museum (Nat. Hist.). Shortly after the publication of Watson's (1937) paper, Dr C. Tate Regan restudied specimens in the British Museum (Nat. Hist.) with a view to contesting Watson's interpretation of the exoskeleton of the branchial region. Unfortunately Regan died before this work was finished, and although Dr E. I. White attempted to edit his notes for publication, this proved impossible. Later Holmgren (1942) published on the acanthodian head, and reached similar broad conclusions to Regan. I have carefully read Regan's manuscript, and although our interpretations do not always agree, I am indebted to him for a number of stimulating observations.

An account of the head of *Climatius reticulatus* must be based on BM P.1343 (misquoted throughout by Watson as 38596) and its counterpart RSM 1891.92.198, from the Lower Old Red Sandstone of Turin Hill, Angus, Scotland. This fish reveals the skeleton of the head in an unusually complete state. It is crushed flat and has been split open so that P.1343 shows the exoskeleton of the skull-roof, right cheek, lower jaw and branchial region, all in visceral view (Text-fig. 5; Pl. 2); whilst RSM 1891.92.198 (Watson 1937, Pl. 5, fig. 1) shows an impression of the right branchial



TEXT-FIG. 5. *Climatius reticulatus* Agassiz. Lower Old Red Sandstone. Plan of head; key-diagram for Pl. 2. BM P.1343. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

region and part of the skull-roof, the right gular tesserae in visceral view and part of the meckelian cartilage. The roofing (tectal, *tt*) tesserae are somewhat disturbed anteriorly and confused with the mandibular teeth (*t*), posteriorly the left and right shoulder-girdle bones (*shg*) have been displaced forwards into the branchial region, and the cheek has been pulled away slightly from the roof. Nevertheless the cheek



TEXT-FIG. 6. *Climatius reticulatus* Agassiz. Lower Old Red Sandstone. A, tectal tesserae, after RSM 1887.35.5A. B, ornamentation of circumorbital plate, after RSM 1887.35.5B. C, tessera from interorbital position, after BM.38596. D, visceral surface of lowest tessera of postorbital projection, after BM P.1343. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

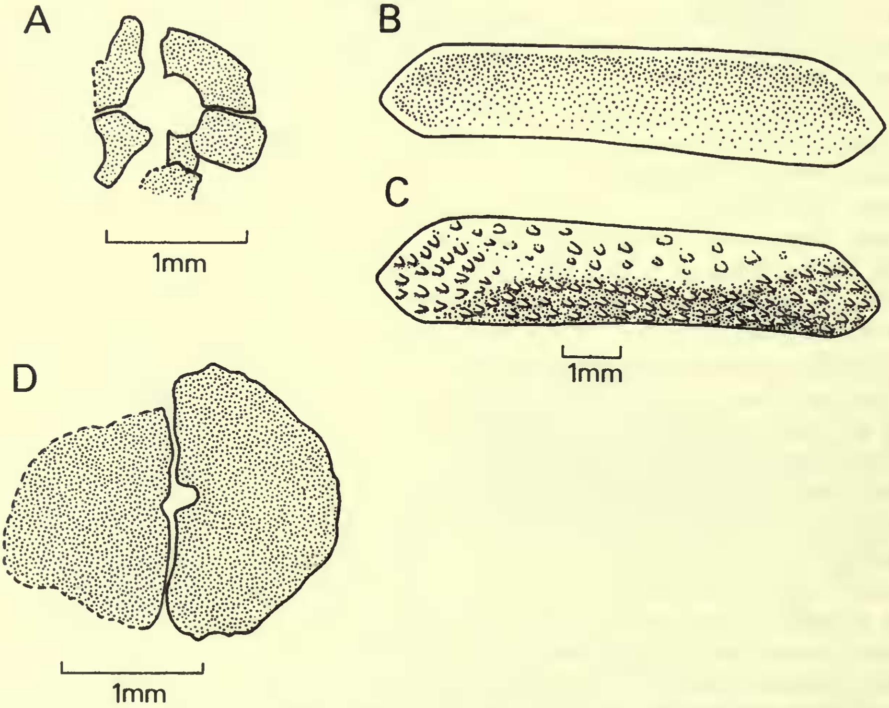
and branchial regions are little disturbed, and appear to show their true relationships and structure. The ornamentation of the tesserae and the structure of the jaw cartilages must be taken from other specimens. Watson (1937 : 52) has accurately described the granular appearance of the jaw cartilages; they have neither the character of perichondral bone nor of chondrichthyan calcified cartilage, and are of uncertain composition. Ørvig's (1951 : 412–415) study of other genera, however, suggests that they may be subperichondral calcified cartilage.

The orbit is surrounded by six transversely arched, stout plates (*cmo*, Text-fig. 5), which comprise two broad dorsals, two narrow ventrals, a small anterior and a posterior. They are ornamented with high, ridged denticle-like tubercles, which tend to fuse in rows across the surface (Miles 1966, Text-fig. 9; Pl. 10, fig. 1). In some specimens the circumorbital plates appear to be composed of fused tesserae, each with one tubercle (Text-fig. 6B; cf. Gross 1971, Pl. 2, figs. 10, 18). Immediately behind the posterior dorsal circumorbital plate a group of large tesserae marks the position of the underlying postorbital process of the neurocranium (*popr*, Text-fig. 5). The large ventral tessera of this group (the postorbital projection of the tectal field) has a deeply concave visceral surface (Text-fig. 6D).

Behind the postorbital group, the tesserae change character markedly at the infraorbital (otic branch) – main lateral-line (*ifc.ot*, *ll*). The lateral-line may conveniently be used to delimit the lateral extent of the tectal tesserae, but the difference in size between the elements above and below the lateral-line led Watson (1937 : 53, 56, also Miles 1966, Text-fig. 9) into the serious error of regarding the upper tesserae as marking the edge of a gill-chamber which stretched from the postorbital projection to the scapular blade. The lower tesserae are not shown in his illustrations (Watson 1937, Text-fig. 1, overlay to Pl. 5, fig. 2) and are discounted as having 'perhaps turned downward to the inner surface of the gill chamber'. Some 15 mm behind the postorbital projection there is a second lateral extension of the tectal tesserae, the prebranchial projection (*pbpr*, Text-fig. 5). Unfortunately this area of the skull-roof is disturbed by the displaced left half of the shoulder-girdle.

The scales of the trunk give way to the tectal field abruptly, along an oblique line which extends from just above the prebranchial projection almost to the otic region in the middle line. The arrangement of the tectal tesserae has been described by Watson (1937 : 53–56). On the outer surface the tesserae bear an ornament of ridged tubercles, which on some plates are still more densely packed than shown in Text-fig. 6A. These plates resemble some of the tesserae coronatae of *Nostolepis striata* Pander, which Gross (1971, Pl. 3, fig. 13) suggests were situated dorsally on the head. More anteriorly, between the circumorbital rings, the character of the plates changes. They become thicker and the tubercles tend to fuse into stout, radiating ridges (Text-fig. 6C; Dean 1907, Text-fig. 15). These plates are similar to certain tesserae stellatae of *N. striata* (Gross 1971, Pl. 2, figs. 25–26), although in this species Gross suggests they come from the underside of the head. The stellate tesserae are particularly well developed along the upper margin of the mouth, under the orbits and across the snout (BM 38596, RSM 1887.35.5c). This belies Watson's remark that the mouth 'has no distinct borders'. Watson described a possible nasal opening in RSM 1891.92.206. A similar fenestra can be seen in BM P.1343a, surrounded by five tesserae (Text-fig. 7A). A striking feature of the snout, as preserved, is the small distance that the tesserae extend in front of the circumorbital rings. This is important in making restorations of the snout, as Watson realised, and with other factors it makes it difficult to accept much of Holmgren's (1942) discussion of the basicranium and snout in acanthodians, which is based on conditions in selachians.

Watson (1937 : 54) has produced evidence of an opening for the ductus endolymphaticus in BM P.1343 (*end*?, Text-fig. 5). 'There is only one recognisable irregularity in the roof of the skull in this region, the presence, a little to each side of the mid-line of a pair of rather larger bones which meet one another in a straight transverse suture. On the left side in this suture there is a very minute foramen whose border lies mainly in the posterior bone; the opening is less clearly seen on the right.' Paradoxically I cannot confirm Watson's (1937, overlay to Pl. 5, fig. 2) interpretation of the tesserae surrounding the foramen in BM P.1343, but I find tesserae of exactly this form in BM 38596 (Text-fig. 7D). I am, however, not convinced that the foramen is the opening of the endolymphatic duct, because the



Text-fig. 7. *Climatius reticulatus* Agassiz. Lower Old Red Sandstone. A, circumnasal plates, BM P.1343a. B, C, branchiostegal ray in visceral and superficial view, restored after BM.38596. D, tectal tesserae surrounding endolymphatic or sensory-line opening, BM.38596. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

lateral-lines of the roof open to the surface through exactly similar foramina, and corroborative evidence of the duct has not been found in other acanthodians. On the present evidence the foramen can equally well be interpreted as the opening of the duct or for the supratemporal sensory line. A more laterally situated foramen in BM P.1343 supports the second view (Text-fig. 5). I do not dissent from Watson's interpretation of the other sensory lines, except to add that the otic branch of the infraorbital line appears to continue forwards above the postorbital tesserae as the 'profundus' line (*pfc*, Text-fig. 10; Miles 1966, Text-fig. 9, interpreted as edge of gill chamber), and there is evidence of the cheek (supramaxillary) line in BM P.6961 (*sml*, Text-fig. 10).

Although they are slightly displaced, the tesserae along the lower margin of the infraorbital (otic branch) – main lateral-line can be followed almost without a break from the postorbital projection (*popr*) back over the gill region (Text-fig. 5). Ventral to these tesserae, between the postorbital and prebranchial (*pbpr*) projections of the tectal field, there is a field of smaller tesserae which has pulled slightly away from the lateral-line. These may be termed the squamosal tesserae (*sqt*). Watson (1937 : 56, Text-fig. 1) interpreted them as having a position in the dorsal region of the mandibular operculum, and in his restoration he depicted the whole field as markedly more extensive than it appears in the fossil. The tesserae seem to be arranged essentially in horizontal rows, except most anteriorly where they increase in size and are navicular (*nt*), and are said by Watson to be 'arranged in a sickle shape'. These anterior elements mark the transition from the small horizontally placed squamosal tesserae to those of the postorbital projection, and it is doubtful whether they have any deeper morphological significance.

Ventral to the postorbital projection of the tectal field and the squamosal field, lie the tesserae of the cheek (*jut*). These jugal tesserae are tesserae stellatae, and except for some slight elongation they are closely similar to those of the roof. Similar tesserae cover the lateral surface of the lower jaw (*mt*), and the two groups were continuous over the adductor mandibulae musculature. The cheek tesserae accurately mirror the shape of the palatoquadrate, with a series of well defined elements attached to the upper rim of this cartilage bone. BM P.6961 shows that Watson erred in stating that the anterior ends of the branchiostegal rays ('mandibular rays') were attached to the outer surface of the jaw bones; they follow immediately posterior to these bones.[1] For the most part the cheek tesserae seem to be arranged in irregular vertical rows, as can be seen in the anterior region of BM P.1343. Posteriorly they are not well seen, but probably the rows have a more diagonal arrangement, like the mandibular tesserae (Watson 1937, Text-fig. 1).

The most ventral mandibular tesserae form two or three rows of low, elongated elements (*mt*), which are transitional to the still smaller, more elongated gular tesserae (*tgu*) on the chin. These tesserae form a pair of lateral fields, and are

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[1] Watson (1937 : 56) writes of 'a series of very large thick bony rays (*Mand. Ray*), whose long dorsal and ventral borders are in contact with one another'. And . . . 'these opercular rays are attached by their anterior ends to the outer surfaces of the articular ends of the palato-quadrate and Meckel's cartilage'. If both of these statements are true it is difficult to see how the fish could have effectively opened its mouth.

arranged 'in festoons parallel to the lower jaw' (Watson 1937 : 56). It is clear, as in other acanthodians, that there are no free-standing gular membranes (Miles 1966 : 153).

In BM P.1343 there are five large branchiostegal rays (*br*) which I have numbered from the most ventral upwards in Text-fig. 5. The whole series has been slightly displaced posteriorly by the shoulder-girdle, but the second ray appears to have been situated at the level of the mandibular joint. In visceral aspect the rays are slightly hollowed and trough-like. On the outer surface they bear a median ridge which is flattened at either end (Text-fig. 7B, C). The branchiostegal rays are ornamented with ridged tubercles, like the tesserae. Above the 5th ray there is a series of smaller elements (*Ha*), which are somewhat disturbed, but probably each element is steeply inclined and the whole series leads up to the prebranchial projection. It is difficult to decide whether the apparent topmost element belongs to this series or to the lower edge of the projection. Behind these smaller rays there is a series of fine tesserae (*Hp*), which is interrupted (post-mortem?) and thus divided into separate dorsal and ventral groups. Comparisons with the succeeding branchial arches (*v. infra*) suggest that the groups of elements labelled *Ha* and *Hp* are related respectively to anterior and posterior exoskeletal series in the dorsal region of the hyoid (i.e., the main) gill-cover, above the branchiostegal rays. Watson's interpretation of the structures in this region is different. He shows a larger, more uniform series of branchiostegal ('mandibular') rays, which extends up to the top of the jugal field of tesserae, where it is contiguous with the squamosal tesserae ('mandibular operculum'). Behind the branchiostegal rays he depicts an extensive group of small tesserae ('ossicles') which extends the ('mandibular') operculum back across the lower region of the branchial region almost to the shoulder-girdle. Ventrally these elements run down into the gular tesserae.

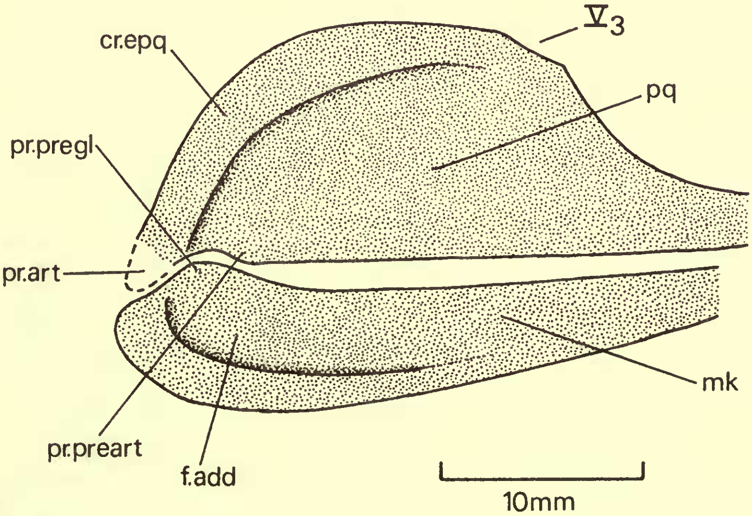
There is evidence of four branchial arches behind the hyoid gill-cover. They appear to be fundamentally the same as each other with respect to the exoskeleton, although their structure is progressively less well seen from the first one backwards. The scales are slightly displaced at the hind end of the branchial region, and it is not obvious that the gill-chamber had a definite posterior margin in the flank squamation. The exoskeleton of each gill-cover comprises an anterior series of elongated, obliquely placed elements (*Ia–IVa*), which are arranged in an irregular echelon; and a posterior series of smaller, more horizontally placed elements (*Ip–IVp*). The posterior elements are subject to some dorsoventral differentiation. Dorsally they increase in size, extend forwards to replace the anterior, oblique elements, and are transitional to the tesserae which form the lower margin of the main lateral-line. Ventrally they appear to dissolve into small scales (*vt*), which are presumably transitional to the scales overlying the scapulocoracoid, although this region cannot be clearly observed. The small ventral scales of the first gill-cover (*Ivt*) were probably included by Watson in the 'mandibular operculum'.

The arrangement of the exoskeleton of the gill-arches can be readily understood if it is assumed that the anterior series of elements were situated on the free ends of the gill-septa, and the posterior series on the outer surface of the gill-flaps.

The jaw cartilages of *Climatius* can be studied in BM P.6961 and GSM 49785 (Pl. 3), on which Text-fig. 8 is based. The details are not clearly seen, but it seems beyond question that Watson was correct in claiming the absence from the palatoquadrate of the otic process found in *Acanthodes*. A shallow notch in the dorsal margin (V_3) may mark the passage of the r. mandibularis trigemini and external carotid artery. The lateral face of the palatoquadrate bears an extrapalatoquadrate ridge (*cr.epq*). There is no sign anteriorly of a basal or orbital process, and no evidence that the palatoquadrate extended forwards in a palatine process to meet its antimere in the middle line (cf. *Acanthodes*, Miles 1968 : 120). The meckelian cartilage bears a lateral fossa for the insertion of the adductor muscles (*f.add*). There is no indication of a dermal mandibular bone. The mandibular joint is obscure, but it is possible that it was double as in *Acanthodes bronni* (Miles 1968), as there is some evidence of a prearticular process of the palatoquadrate (*pr.preart*) and a preglenoid process of the meckelian cartilage (*pr.pregl*).

Most specimens of *Climatius* have the dentition preserved (see e.g. Pl. 3), but the teeth are always so disturbed that it is impossible to obtain a complete picture of their form and arrangement. They seem, however, to be restricted to the lower jaw, and are shown somewhat diagrammatically in Watson's (1937, Text-fig. 1) reconstruction of the head. The dentition is seen more completely in *Ptomacanthus anglicus* and the following notes are given mainly to supplement Watson's account and provide a basis for comparison.

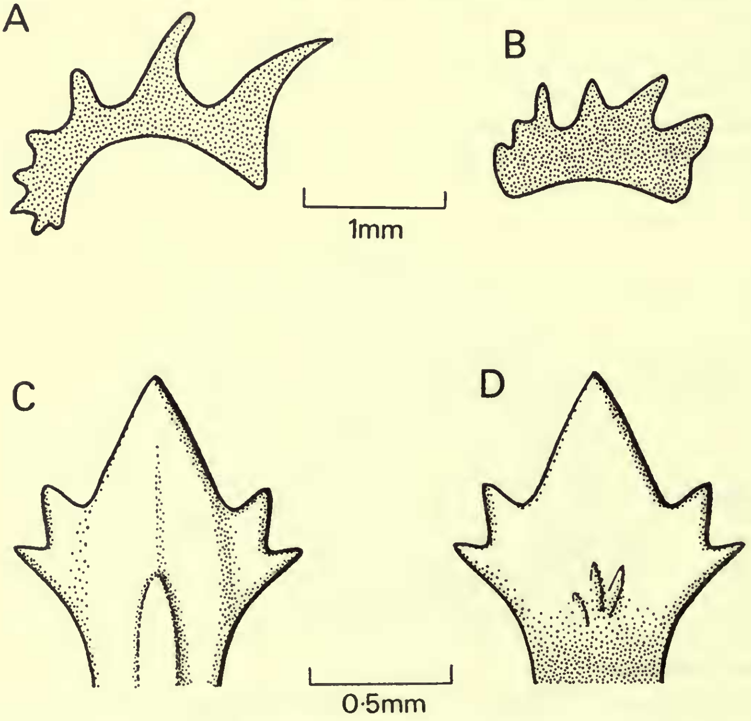
Each tooth has an arched basal plate placed transversely across the margin of the jaw, and a number (maximum at least seven) of cusps (Text-fig. 9; Miles 1966, Pl. 10).



Text-fig. 8. *Climatius reticulatus* Agassiz. Lower Old Red Sandstone. Right palatoquadrate and meckelian cartilage in lateral view. After BM P.6961 and GSM 49785. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

The teeth have usually been split through their substance in the rock, and there appears to be much variation in the thickness of the basal plate and in the length and number of the cusps. The true variation in these respects cannot be estimated. The principal cusps seem clearly to increase in height in the lingual direction, and most labially they have almost the character of the dermal ornamentation. Comparable conditions are found in *Nostolepis* (Gross 1957, 1971). In labial and lingual view the principal tooth cusps are seen to be broad and thin, and to have two pairs of smaller side cusps, which are almost symmetrically placed. Towards the base of each principal cusp the surface is thickened by a broad ridge in some cases, and bears several slender ridges in others. It is tentatively suggested that the first condition is seen on the labial face of the cusp (Text-fig. 9C), and the second on the lingual face (Text-fig. 9D). The broad ridge has been incorrectly labelled as a tooth cusp in an earlier work (Miles 1966, Pl. 10B).

Because of the curvature of the basal plate, it is customary to term the climatiid tooth a tooth-whorl or spiral (see also ischnacanthids), but these names are misleading if they imply the existence of a compound structure. Thus Watson (1937 : 53) writes that the dentition is 'composed of fused whorls of teeth', and the 'whorl



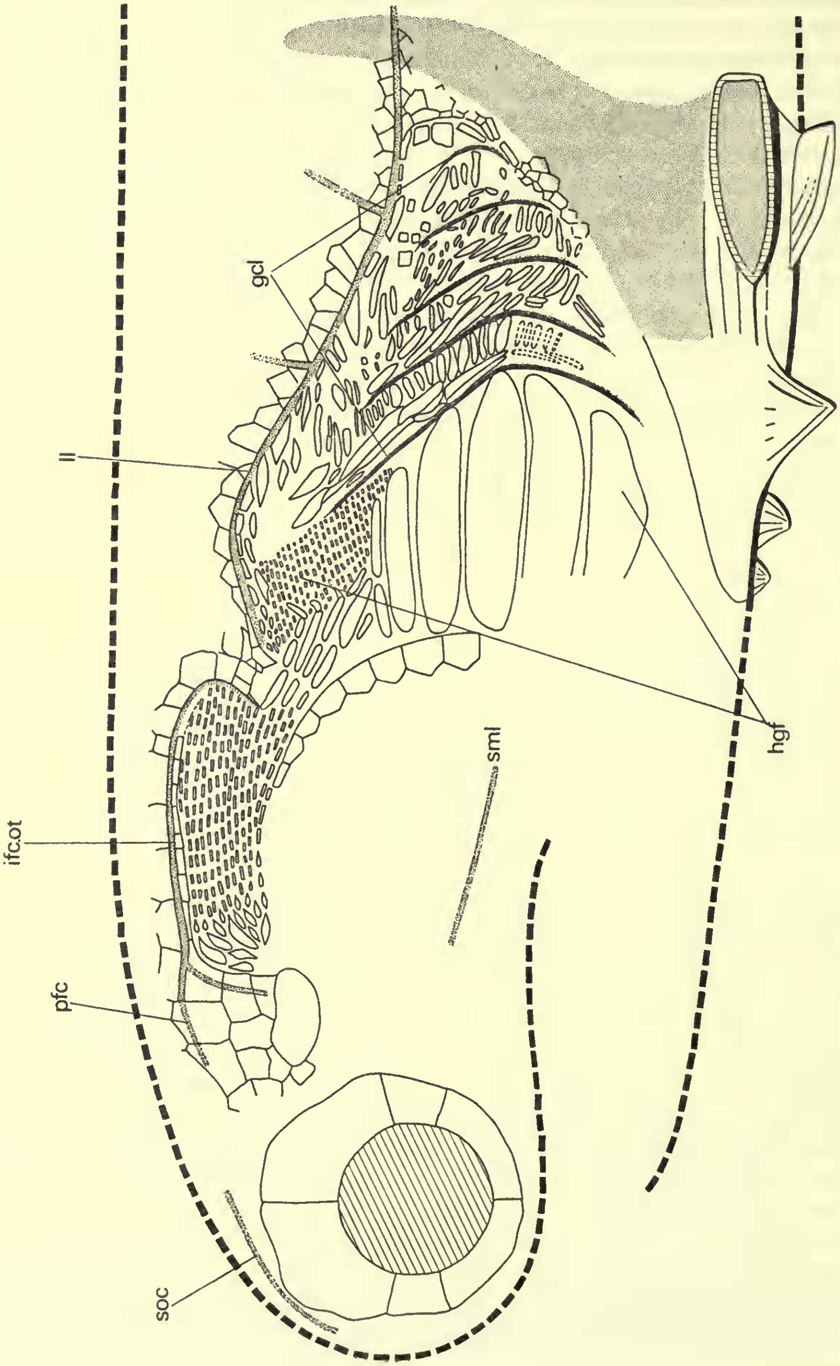
TEXT-FIG. 9. *Climatius reticulatus* Agassiz. Lower Old Red Sandstone. Jaw teeth. A, section after GSM 49785; B, section after BM 38596; C, D, labial and lingual surfaces of cusp respectively after RSM 1887.35.5C and BM P.1343. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

seems to consist of at least three teeth'. I have propagated this error by suggesting that in climatiiforms the teeth apparently 'underwent a regular replacement which simulated the elasmobranch method' (Miles 1965 : 245, also 1971 : 68). However, Gross (1957 : 7) has suggested that all the cusps ('teeth') of the tooth ('spiral') were formed at the same time; that the growth of the tooth did not involve the addition of new cusps; and there is no evidence of tooth replacement. The absence of replacement in climatiids is confirmed by the specimens of *P. anglicus* described below. The teeth are thus not closely comparable with those of elasmobranchs. Whether these remarks also apply to the tightly inrolled teeth of primitive ischnacanthids (*Gomphodus*) is not clear (Woodward 1891, Pl. 15, fig. 1; Gross 1957, Pl. 2, figs. 1, 2, Pl. 3, figs. 1, 4), but Gross (1971 : 28) has recently suggested that even teeth of the *Nostolepis* type could grow by the addition of new cusps.

The dentigerous jaw bones of *Nostolepis* and ischnacanthids (Gross 1957, 1971; Ørvig 1967) can be regarded as equal to a series of *Climatius* teeth which have fused together and undergone marked differentiation of the cusps. Ørvig (1967 : 147) stresses that each principal cusp and its side cusps in these jaw bones represents a single tooth, and not a family of teeth ('Zahnfamilien') as originally supposed by Gross (1957 : 12, but see 1971 : 26). Thus, there are no true *marginal tooth-bearing bones* in acanthodians (Miles 1965 : 244), as this expression is normally understood (e.g., Westoll 1949 : 159).

I do not think it is possible to draw an accurate restoration of the head of *Climatius* with the materials now available. Text-fig. 10, therefore, claims to be no more than a diagrammatic attempt to represent the gill region, in which the mutual relations of the main bones are correct in principle. It is based on BM P.1343, and no allowance has been made for the curvature of the cheek and gill region that must have been present in life. Five separate gill-clefts (*gcl*) are shown decreasing in size in the posterior direction. They resemble the gill-clefts of elasmobranchs, but this condition of the branchial openings has long been thought to be primitive for gnathostomes (e.g. Goodrich 1909 : 95). On the other hand, the enlarged first gill-flap (*hgf*) with large branchiostegal rays foreshadows the osteichthyan condition. The enlarged first gill-flap has the same morphological relationships as the hyoidean gill-cover of other fishes, and I reject Watson's conclusion that it belongs to the mandibular arch. The small tesserae in the dorsal part of the hyoid gill cover are not repeated in the more posterior arches. They may indicate the presence of a dorsal fold of flexible skin in this region, shaped somewhat like the fold in the hyoidean gill-flap of *Chlamydoselachus* (Allis 1923, Pl. 1; Smith 1937). In the post-hyoidean gill-arches the tesserae in the skin above the gill-clefts are loosely arranged, and show no definite pattern. Probably this indicates a flexible area, with the tesserae lying superficial to the dorsal constrictor muscles. By an extension of this argument, the squamosal field of tesserae may be related to that part of the dorsal constrictor musculature of the mandibular arch which passed from the palatoquadrate to the brain-case (m. levator palatoquadrati; cf. *Acanthodes*, Miles 1968 : 117).

Perhaps the most telling criticism of Watson's restoration is that it is not functionally convincing. Thus by Watson's own declaration the palatoquadrate has no



TEXT-FIG. 10. *Climatius reticulatus* Agassiz. Lower Old Red Sandstone. Sketch restoration of head in lateral view.

contact with the neurocranium[2], the hyoid arch is unmodified and non-suspensory, and the region above the palatoquadrate, which I believe was crossed by the mandibular levator muscles, is perforated by the anterior part of a very long, open spiracular gill-slit. If these conditions obtained, it is difficult to see how the upper jaw was held firmly in place in the head, or how it could have carried a large, mobile gill-cover.

The new restoration (Text-fig. 10) removes the evidence for a complete spiracular gill-slit and unmodified hyoid arch. There is no direct evidence bearing on the condition of this last structure, but the nature of the palatoquadrate suggests the presence of a suspensory hyomandibula, as in *Acanthodes*, and I believe that the jaw suspension was hyostylic.

(vii) *Head of Ptomacanthus anglicus*. The exoskeleton is well shown by P.24919 (Pls. 5, 6), and a number of points are confirmed by P.19998–9 and P.20002–3. There is, however, no sign of the lateral-line system. There is a stout circumorbital ring (*cmo*, Pl. 1, fig. 2, Pl. 5) with an undetermined number of plates, although there is evidence of two broad dorsal plates as in *Climatius*. Dorsally the trunk scales extend forwards over the branchial skeleton into the otic region. Here, as in *Climatius*, they are replaced by thick tectal tesserae (*tt*, Pl. 5). On the anterior surface of the snout the tesserae are enlarged into tesserae stellatae, whilst on the ventral margin they form a distinct row of smaller elements which interlock with the anterior teeth of the upper jaw (Pl. 6). A paired break in the tesserae of the snout is probably the exoskeletal nasal opening (*na*). There is no sign of the postorbital or prebranchial projection of the tectal field.

The tectal tesserae are not as distinctly separated from the jugal (*jut*) and squamosal (*sqt*) tesserae as in *Climatius* (Pl. 5). The different fields grade into each other over short distances. The jugal tesserae are tesserae stellatae. They are slightly larger than the tectal tesserae, and ventrally they merge with the large mandibular tesserae over the surface of the lower jaw (*mt*, Pl. 5). The last elements are arranged in rows much as shown by Watson for *Climatius*. The field of small jugal tesserae is, however, more extensive ventrally than in *Climatius*. Behind the lower jaw there are five slender branchiostegal rays (*br*, Pls. 5, 6), with an ornament of short, interlocking ridges on the outer surface. The more dorsal region of the hyoid gill-cover is unknown. Ventrally the mandibular tesserae give way to elongated gular tesserae (*tgu*, Pl. 6) closely similar to those of *Climatius*, but the lower surface of the head is not well preserved. It is possible that there are four gill arches behind the hyoid gill-cover, although the exact number cannot be given. The exoskeleton of each comprises an anterior series of upright elements (*br.a*) and a posterior series of horizontal elements (*br.p*, Pl. 6). These elements are stouter, and apparently more closely and regularly arranged than their homologues in *Climatius*, although this may simply be a matter of superior preservation in *P.*

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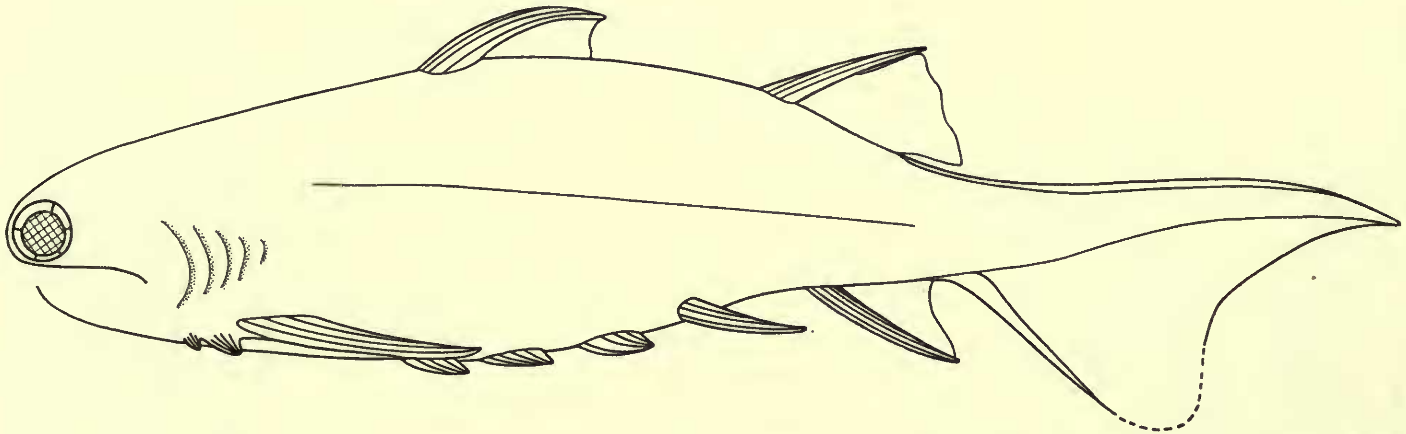
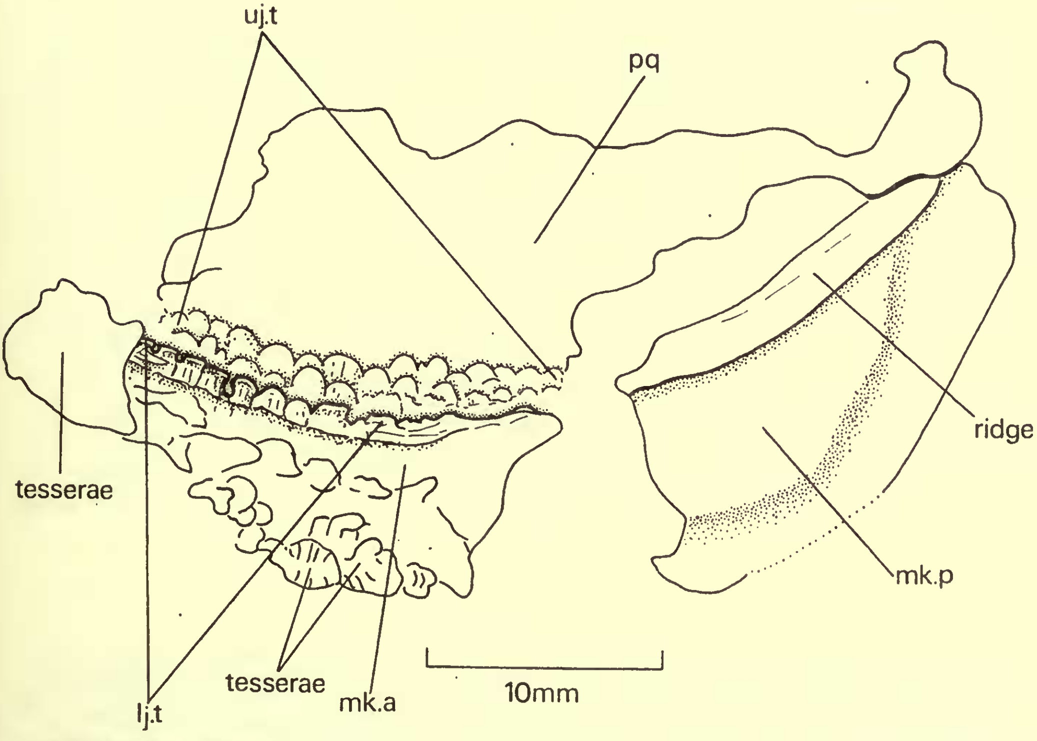
[2] I think there may have been a basal articulation, as in *Acanthodes*, even though there is no evidence of a basal process in the incomplete fossils.



TEXT-FIG. 11. *Ptomacanthus anglicus* gen. et sp. nov. Lower Old Red Sandstone. Restoration in lateral view.

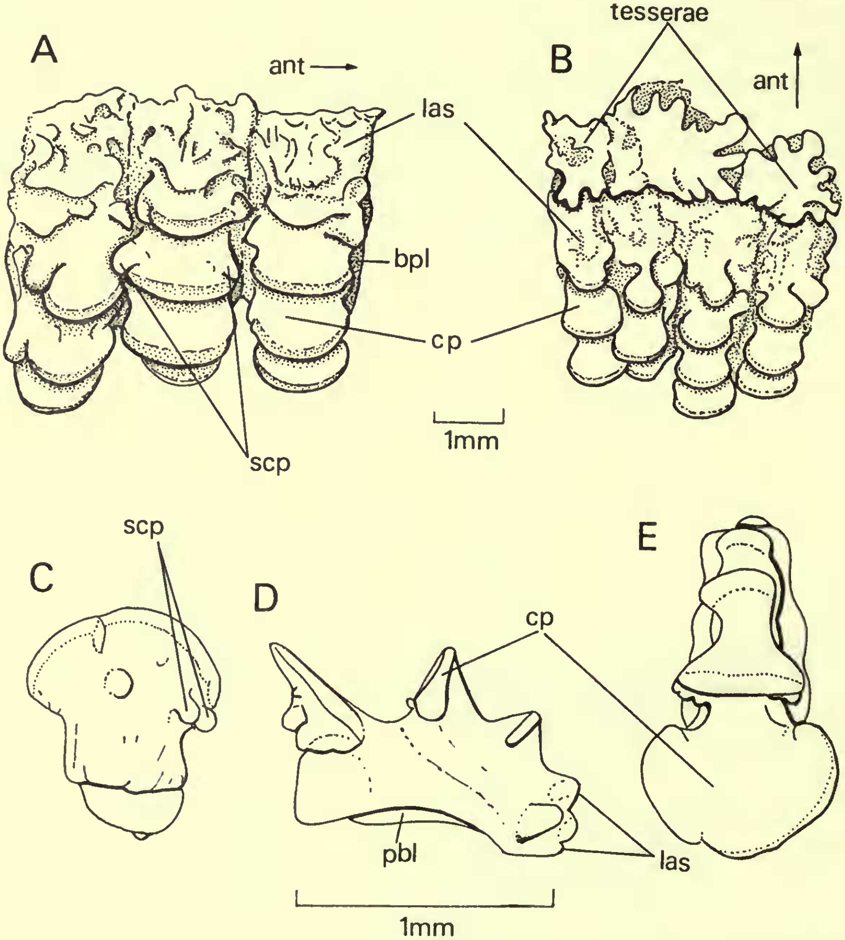
anglicus. There is no evidence of clear-cut margins to the gill-chamber in the exoskeleton, and this supports the new interpretation of *Climatius* given above.

In P.19998 the jugal and mandibular tesserae are pressed down over the outer surfaces of the right palatoquadrate and meckelian cartilage. The relief clearly shows the presence of a stout extrapalatoquadrate ridge and an adductor muscle fossa, as in *Climatius*. The palatoquadrate is also seen in other specimens (*pq*, Text-fig. 12, Pl. 1, fig. 2, Pl. 6), which confirm the lack of a palatine process and indicate a close similarity to *Climatius*, but add no details of structure. P.19999 (Pl. 4, fig. 1, use Text-fig. 12 as key-drawing) shows both the palatoquadrate and meckelian cartilage and demonstrates that there are teeth in both the upper and lower jaws (cf. *Climatius*, p. 131). The meckelian cartilage is calcified in separate anterior (*mk.a*, mentomandibular) and posterior (*mk.p*, articular) elements, as it is in a number of ischnacanthiform and acanthodiform genera (Watson 1937; Miles 1966, 1968), although this condition has not hitherto been recorded in a climatiiform. The lower jaw teeth extend along the full length of the anterior element; the dorsal margin of the posterior element is thickened into a ridge. There is no dermal mandibular bone on the lower margin of the jaw.



TEXT-FIG. 12. *Ptomacanthus anglicus* gen. et sp. nov. Lower Old Red Sandstone. Left lower jaw and palatoquadrate; key-diagram for Pl. 4, fig. 1. BM P.19999. Ditton Series, Wayne Herbert quarry, Newton, Herefordshire, England.

The teeth are best seen in P.24919a, which is illustrated by a photograph (Pl. 6). The upper teeth are preserved in an almost undisturbed arch, and comprise multicuspid structures which can be interpreted by comparison with the detached teeth of *Nostolepis striata*, which they closely resemble (Text-fig. 13; Gross 1957, Pl. 4, figs. 6, 7, 1971, Pl. 3, figs. 32–34). There is, however, no evidence in either the upper or lower jaws of the dentigerous jaw bones found in *N. striata* (Gross 1957, 1971; Ørvig 1967). The tooth row is continuous across the middle line and includes about 50 separate teeth packed closely together. The most anterior teeth measure



TEXT-FIG. 13. A, B, *Ptomacanthus anglicus* gen. et sp. nov. Lower Old Red Sandstone. Groups of teeth in ventral view, from the lateral and rostral regions of the upper tooth arcade respectively, in B with adjacent tesserae. BM P.24919a. Ditton Series, Wayne Herbert quarry, Newton, Herefordshire, England. C, D, E, *Nostolepis striata* Pander. Upper Silurian. Tooth in lingual, anterior (or posterior) and dorsal view respectively. After Gross 1957, Pl. 4, fig. 7.

about 0·8 mm across the broad face of their largest cusps; from which the teeth increase in size posteriorly until this dimension is about 1·7 mm.

The individual teeth have an arched basal plate (*bpl*, Text-fig. 13A, B) with three or four blade-like cusps (*cp*); small polyp-like side cusps (*scp*) are also present on some teeth, as in *Nostolepis*. The labial surface of each tooth (*las*) is ornamented like the adjacent tesserae, and the teeth and tesserae are firmly interlocked with each other. This is conclusive evidence that the teeth were not elasmobranch-like, but were permanent growing units (p. 133), and it explains how the teeth were supported in a continuous row over the anterior margin of the upper jaw in the absence of a palatoquadrate symphysis (p. 137). Only the larger, more posterior teeth received additional support from the palatoquadrate, and it was these teeth that carried the main force of the bite. Unfortunately, the curvature of the basal plates is unknown, and the data provided by Gross (1957) cannot be related to the positions of the teeth in the jaws. It seems probable that the cusps of adjacent teeth were accurately aligned, so that they formed ridges following the margin of the jaw, but it is not possible to demonstrate this conclusively. It does seem clear, however, that all the cusps were functional and that the upper teeth accurately 'interdigitated' with those of the lower jaw.

DISCUSSION. The teeth, scales, tesserae and spines show that *Ptomacanthus* is a relatively primitive climatiid closely related to *Nostolepis* and *Climatius*. It differs from *Nostolepis* in the absence of dentigerous jaw bones, although the significance of this cannot be assessed, and resembles it strikingly in the form of the discrete marginal jaw teeth. This resemblance may indicate immediate consanguinity, as I believe, or may be due to parallel evolution. Further comparisons and conclusions can hardly be drawn in the absence of articulated specimens of *Nostolepis*. The above account has shown that *Ptomacanthus* and *Climatius* are fundamentally the same in the skeleton of the head. *Climatius* is, however, more advanced in the dentition, as it lacks upper jaw teeth, and more primitive in its heavily ossified shoulder-girdle (p. 163). *Erriwacanthus* (p. 166) is also more primitive than *Ptomacanthus* in the structure of the shoulder-girdle.

Of the more advanced climatiids, *Ptomacanthus* differs from *Brachyacanthus* in the absence of enlarged median dorsal scutes in front of the first dorsal fin-spine and in its longer fin-spines; and from *Parexus* in the absence of a greatly lengthened first dorsal fin-spine and in the structure of the shoulder-girdle (p. 181).

VERNICOMACANTHUS gen. nov.

DEFINITION. Climatiid fishes with an elongated body and moderately broad fin-spines; anterior dorsal fin-spine slightly curved and longer than pectoral fin-spine, but not as elongated as in *Parexus*; dermal shoulder-girdle reduced to anterior lorical, and ascending lamina of a compound pinnal plate, and with at least one paired prepectoral spine.

Etymology. After the *Vernicomes*, the Caledonian tribe which inhabited that part of Southern Pictavia which is now in Angus, Scotland; and Gr. *akantha*, a thorn.

Type species. *Climatius uncinatus* Powrie.

Remarks. *Vernicomacanthus* differs from *Climatius* in the structure of the shoulder-girdle (pp. 162–166; q.v. for terminology), and in the same way from *Erriwacanthus*, *Ptomacanthus* and *Brachyacanthus*. It is probably more closely related to *Parexus*, from which, however, it differs in the length of the first dorsal fin-spine. It also differs from *Brachyacanthus* in the absence of median scutes in front of the first dorsal fin-spine. *Vernicomacanthus* has up to six pairs of intermediate spines, i.e., the same number as some specimens of *Euthacanthus macnicoli* (Watson 1937 : 65) but more than any other articulated climatiid.

VERNICOMACANTHUS UNCINATUS (Powrie)

Pl. 7

1864 *Climatius uncinatus;* Powrie (ex Egerton MS), p. 422
1870 *Climatius uncinatus;* Powrie, p. 296, pl. 14, fig. 11
1891 *Climatius uncinatus;* Powrie, Woodward, p. 30

Definition. A species attaining a length of 150 mm, with large curved pectoral spines bearing posterior denticles, and with six pairs of well-developed intermediate spines.

Type. The lectotype is RSM 1891.92.208 (Powrie 1870, Pl. 14, fig. 11).

Material. BM P.1342a, P.6960, P.1342; R S M 1891.92.209 and Kinnaird 82 (counterparts), 1891.92.210 and Mitchell 57 (counterparts).

Locality. Turin Hill, Angus, Scotland.

Horizon. Arbuthnott Group, Dundee Formation, Lower Old Red Sandstone.

Remarks. The shoulder-girdle of this species is described below (pp. 176–180). The exoskeleton of the head is closely comparable with that of *Climatius reticulatus*, and several specimens (e.g. Pl. 7) confirm that Watson mistook lateral-lines of climatiids for the dorsal margin of the gill-chamber. The exoskeletal elements of the head are labelled in Pl. 7 to facilitate a direct comparison with the figures of *C. reticulatus* (Text-figs. 5, 10, Pl. 2).

VERNICOMACANTHUS WAYNENSIS sp. nov.

Pl. 1, figs. 1, 3, Pls. 8–10

Etymology. After Wayne Herbert quarry.

Diagnosis. A species differing from the type, *V. uncinatus*, in its greater size and in the lack of posterior denticles on the pectoral fin-spines, in the absence of a median prepectoral spine, in the reduction of the anterior lorical, and in the separation of this last plate from the ascending pinnal lamina.

TYPE. The holotype is an almost complete fish in part and counterpart, BM P.24938a, b (Pl. 1, figs. 1, 3, Pls. 8, 9, fig. 2).

HORIZON. Ditton Series, about 66 m above the main '*Psammosteus*' limestone, in the *Pteraspis crouchi* zone.

LOCALITY. Wayne Herbert quarry, near Newton, SW. Herefordshire; in the siltstone lenticle described by White (1935 : 383).

MATERIAL. This account is based on six individuals in the British Museum (Nat. Hist.); P.24938a, b, the holotype; P.16614, part of the flank in the region of the shoulder-girdle; P.16615, the ventral region of the flank with the dermal shoulder-girdle and the most anterior intermediate spines; P.52441a (Pl. 9, fig. 1), b (Pl. 10), most of the body forwards from the anal fin-spine to the branchiostegal rays, on the same slab as a specimen of *Pteraspis rostrata* figured by White (1935, Pe. 27, fig. 107); P.52443, the ventral region of the trunk with the intermediate spines.

DESCRIPTION. (i) *General features*. *V. waynensis* is a climatiid of moderate size, which reached a length of at least 140 mm. Incomplete preservation rules out a table of measurements of the fin-spines. The preservation of the specimens is comparable with that of *Ptomacanthus anglicus*, and it suggests a moderately slender body with a flattened venter and a broad skull-roof. It is difficult to obtain an accurate picture of the whole fish (Text-fig. 16), but it appears that the body is more elongated than in other genera of climatiids, and in this respect is comparable with *Euthacanthus* (Watson 1937, Text-fig. 4). In both *Vernicomacanthus* and *Euthacanthus* the length of the body and the large number of intermediate spines are probably correlated. There are six pairs in *V. waynensis* as in *V. uncinatus*. The pectoral and pelvic fin-spines are situated slightly in front of the transverse planes of the anterior and posterior dorsal fin-spines respectively (contrast *Euthacanthus*), and the anal fin-spine is inserted posterior to the level of the posterior dorsal (Pl. 1, fig. 1).

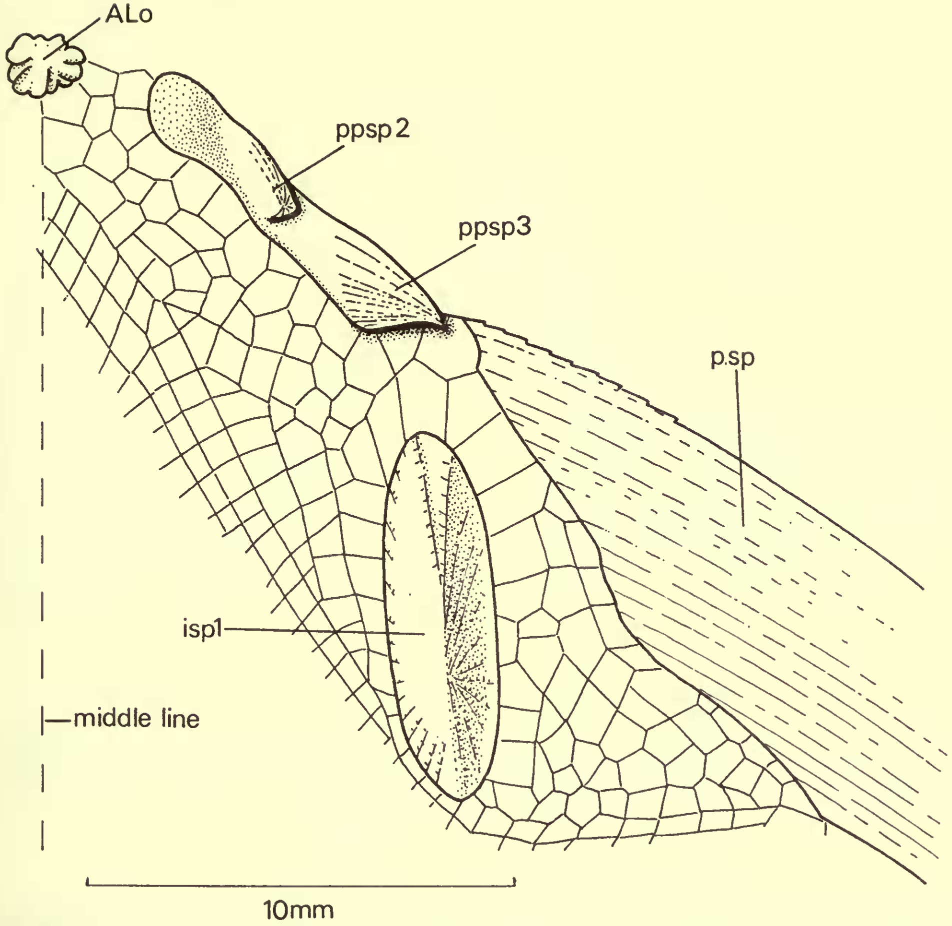
(ii) *Squamation*. The scales are typically acanthodian and encircle the body in oblique rows in the usual way (Pl. 1, fig. 1, Pls. 8, 10). The flank and ventral scales have the crown ornamented with a large central ridge, and one or two pairs of smaller side ridges, all of which are striated and end in free standing points (Pl. 1, fig. 3). The length of the crown is about 0·5 mm on the flank of the holotype. Towards the median dorsal line the scales increase in size, to almost twice their size on the flank (Pl. 1, fig. 1, Pl. 10), and the ridges become broken up into a network of connected tubercles. Enlarged scales are also found at the bases of the spines and on the lateral face of the scapulocoracoid (Pl. 1, fig. 1, Pls. 9, 10). The ventral surface of the body in the region of the pelvic and anal fin-spines is seen in P.52441a (Pl. 9, fig. 1). The vent cannot be satisfactorily delineated, but evidently it was not surrounded by special scales (p. 121). The left ventral lateral-line runs between rows of scales mesial to the intermediate spines in P.24938b (*vll*, Pl. 8). No other lateral-lines can be seen on the head or the trunk. The web of the right pelvic fin is seen in P.52441a (*pv.f*, Pl. 9, fig. 1). It is coated with rows of small scales which appear to be similar to the adjacent body scales. The other fins, including the caudal, are unknown.

The sculptured crowns of the flank scales do not recall closely any other genus (*V. uncinatus* is undescribed in this respect). They have a general resemblance, however, to the scales of *Nostolepis gracilis* figured by Gross (1947, Pl. 26, figs. 1–4). The larger body scales from the median dorsal region, shoulder-girdle and bases of the fin-spines are intermediate in sculpture between the flank scales and tesserae of the head. They are not unlike a figured scale of *N. robusta* (Brotzen), although they are more sparsely ornamented (Gross 1971, Pl. 6, fig. 17).

(iii) *Spines.* The relative lengths of the fin-spines are unknown, but they have been estimated for Text-fig. 16. None is deeply embedded in the body wall. The pectoral spine is less strongly arched than in *V. uncinatus*, and it lacks posterior denticles (*p.sp*, Pl. 1, fig. 1, Pls. 8, 9, fig. 2, Pl. 10). It is ornamented with at least 17 fine, beaded ridges on its dorsal and ventral surfaces. Near the anterior margin these ridges are more robust and have the typical climatiid noded ornamentation. The pelvic (*pv.sp*) and anal (*a.sp*) spines have a similar length and are ornamented with numerous fine beaded ridges; they are only slightly curved. The anterior dorsal spine is slightly curved and probably of similar length to the pectoral. It is probably longer than the posterior dorsal, which is almost straight. Both of the dorsal spines are ornamented with numerous fine, beaded ridges, which proximally dissolve into tubercles, as in the case of the pectoral spine. Of the six pairs of intermediate spines, the first (*isp1*, Text-fig. 14) is large and situated below the scapulocoracoid. The second (*isp2*) and sixth (*isp6*) are vestigial in P.24938a, b (Pl. 1, fig. 1, Pl. 8). In P.52441a, b, however, the sixth is well developed, and although it cannot be seen completely, the second also appears to be a large spine (Pl. 9, fig. 1, Pl. 10). Variation in the number of intermediate spines has been noted by Watson (1937 : 61, 65) in *Climatius reticulatus* and *Euthacanthus macnicoli*, and it may be a common phenomenon in climatioids, although it is worth stressing that it is often difficult to make an accurate count of these spines. Each intermediate spine is ornamented on both sides with about 13 beaded ridges, which converge on the tip.

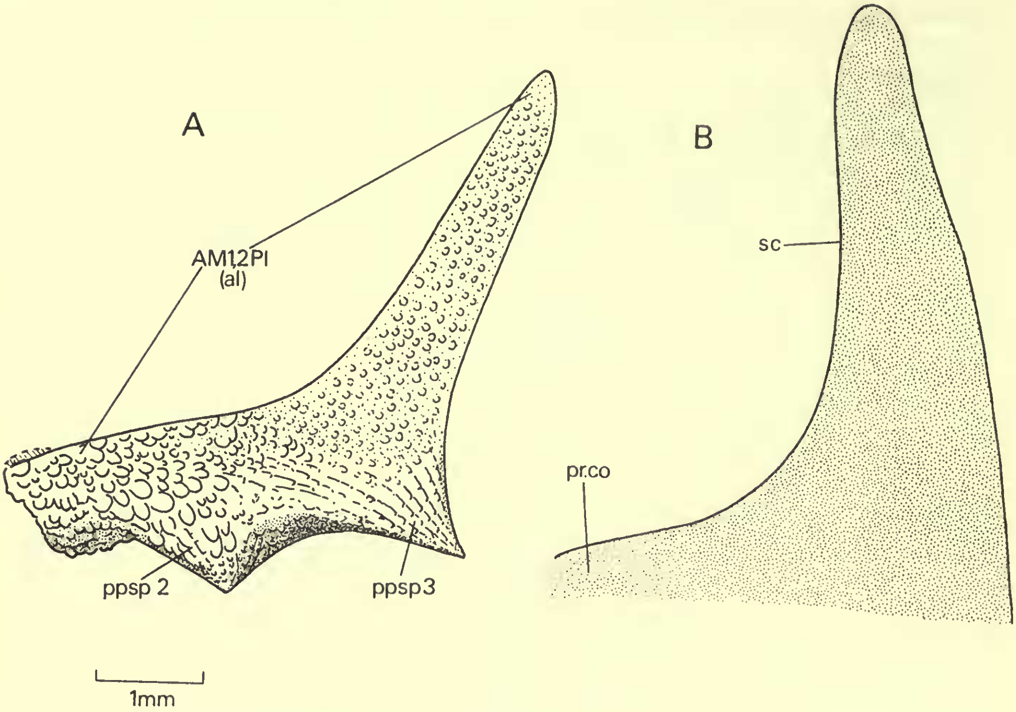
(iv) *Shoulder-girdle.* The dermal shoulder-girdle is represented by the paired ascending lamina (A*M1,2Pl*, Text-fig. 15A, Pl. 1, fig. 1, Pl. 10), which was situated in the postbranchial wall against the scapulocoracoid, and by a separate median ventral tessera (*ALo*, Text-fig. 14, Pl. 9, fig. 2). The ascending lamina bears two ventrolaterally-directed paired prepectoral spines (*ppsp2*, *ppsp3*). The homologies of these elements are discussed below (p. 180). There are no paired ventral plates. The areas between the median tessera and the various spines are filled by a mosaic of enlarged scales (Text-fig. 14, Pl. 9, fig. 2). The scapulocoracoid is covered on its lateral surface by closely applied, enlarged scales. In its general features this structure is like the scapulocoracoid of *V. uncinatus* (Text-fig. 33B), with a moderately broad scapular blade (*sc*, Text-fig. 15B) and a coracoid process (*pr.co*). The coracoid region is unknown.

The exact relationship of the dermal ascending lamina to the scapulocoracoid is unknown. However, its arched form matches that of the anterior margin of the



Text-fig. 14. *Vernicomacanthus waynensis* gen. et sp. nov. Lower Old Red Sandstone. Plan of ventral surface of the body in the region of the right shoulder-girdle. After holotype, BM P.24938. Ditton Series, Wayne Herbert quarry, Newton, Herefordshire, England.

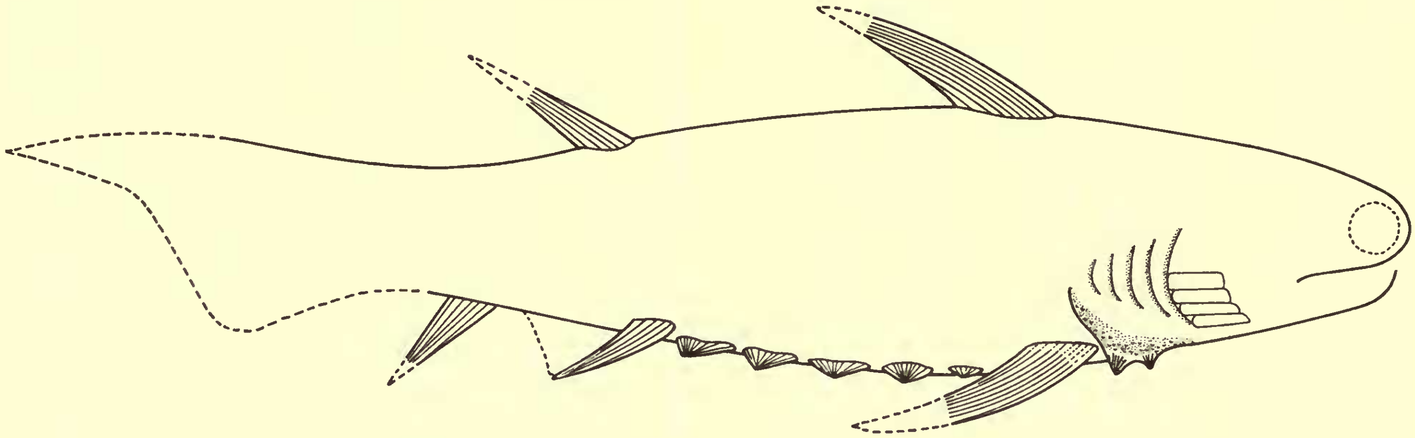
scapulocoracoid, and it seems likely that the dermal element was placed just in front of the scapula so that the coracoid process projected forwards mesially to the paired prepectoral spines. The posterior paired prepectoral spine (*ppsp3*) must have been carried immediately in front of the pectoral spine (Text-fig. 16). The ornamentation of flattened tubercles on the ascending lamina (Text-fig. 15A, Pl. 1, fig. 1, Pl. 10) supports this interpretation, as a similar ornamentation is found in comparable positions in more completely ossified climatiid shoulder-girdles (Text-fig. 29A).



Text-fig. 15. *Vernicomacanthus waynensis* gen. et sp. nov. Lower Old Red Sandstone. A, dermal shoulder-girdle, left, in lateral view. After BM P.17522. B, plan of scapulocoracoid, left, in lateral view. After holotype, BM P.24938. Ditton Series, Wayne Herbert quarry, Newton, Herefordshire, England.

(v) *Head.* The exoskeleton of the head is incompletely seen in P.24938a, b (Pl. 1, fig. 1, Pl. 9, fig. 2). It comprises tesserae stellatae (*tt.mt*) which show little regional variation, other than in their size. The largest elements are in the rostral and mandibular regions. The same specimen has a definite series of lower jaw teeth (*t*, Pl. 9, fig. 2). It is not known whether this species possessed upper jaw teeth. As in *Nostolepis* and *Ptomacanthus* the teeth are arched plates with three or four blade-like cusps, but unfortunately the details of their structure cannot be worked out. Their presence may indicate that *V. waynensis* is closely related to *Nostolepis* and *Ptomacanthus* (but see p. 200). If not, they weaken the evidence I have used to relate these last two genera (p. 139). Teeth are present in the lower jaw of *V. uncinatus*, but their detailed morphology is unknown. In P.52442 there are the remains of four spathiform branchiostegal rays, seen in visceral view. They have been restored diagrammatically in Text-fig. 16 (cf. *V. uncinatus*, Pl. 7).

Discussion. *V. uncinatus* and *V. waynensis* are undoubtedly similar fishes in their gross morphology, and they appear to be closely related. This conclusion is supported by a comparative study of the shoulder-girdle (*v. infra*), which also



Text-fig. 16. *Vernicomacanthus waynensis* gen. et sp. nov. Lower Old Red Sandstone. Restoration in lateral view.

suggests a fairly close relationship between *Vernicomacanthus* and *Parexus*. Whether or not *V. uncinatus* and *V. waynensis* are congeneric is still an open question. However, *V. uncinatus* is quite distinct from *Climatius reticulatus*, and it seems better to include both *V. uncinatus* and *V. waynensis* in a single new genus, than arbitrarily create two new genera for these species, in our present inadequate state of knowledge.

Order ISCHNACANTHIFORMES

Family **ISCHNACANTHIDAE**

URANIACANTHUS gen. nov.

Etymology. *Urania*, Daughter of Oceanus and Tethys [Myth]; Gr. *akantha*, a thorn.

Definition. Ischnacanthiforms with two pairs of intermediate spines, and with the anterior dorsal fin-spine longer than the posterior dorsal.

Type species. *Uraniacanthus spinosus* sp. nov.

Remarks. The classification of this genus and the definitions of some ischnacanthid taxa are discussed below.

URANIACANTHUS SPINOSUS sp. nov.

Pl. 11–13

1956 (?) cf. *Diplacanthus;* Denison : 394

Etymology. L. *spinosus*, spinous.

Diagnosis. The sole species referred to the genus.

Type. The holotype is BM P.16609 (Pl. 11), a small individual with an almost complete trunk but lacking the head.

Horizon. Ditton Series, about 66 m above the main '*Psammosteus*' limestone, in the *Pteraspis crouchi* zone.

Locality. Wayne Herbert quarry, near Newton, SW. Herefordshire; in the siltstone lenticle described by White (1935 : 383).

Material. This account is based on six specimens in the BM; P.16609, the holotype; P.16610–1, the flank of a fish in part and counterpart (on the back of this block are a scapulocoracoid and pectoral spine referred to *Vernicomacanthus waynensis*, which have not been described, and an undetermined meckelian cartilage); P.16612–3, the head and pectoral region in part and counterpart (Pl. 13); P.20000–1, the posterior region of the body with well-preserved caudal, anal and posterior dorsal fins, in part and counterpart (Pl. 12) (P.20000 is on the same block as the type of *Ptomacanthus anglicus*, P.19999); P.53030–1, an incomplete, distorted trunk in part and counterpart; P.53032–5, a body wanting the tail and much of the head, but with associated jaws. A seventh specimen (P.16609) may belong to this species, but it is preserved as a poor impression and has not been considered.

Description. (i) *General features.* With the exception of the dorsally flattened head and shoulder-girdle in P.16612–3 (Pl. 13), the specimens are laterally compressed with the ventral wall tending to be turned in the same plane as the flank (Pl. 11). This suggests that the body was suboval in section with a broad venter between the paired fin-spines, and with a broad skull-roof. The holotype is estimated to have been about 80 mm long, but other specimens show that this species reached at least 150 mm. Measurements of fin-spines are given in Table 2, but the paucity of material and the problem of making accurate measurements preclude an estimate of the variation in their relative proportions. The spines are long and slender. The anterior dorsal (*ad.sp*) is longer than the posterior dorsal (*pd.sp*) and is situated just posterior to the shoulder-girdle. The pelvic spines (*pv.sp*) are inserted well in front, and the anal spine (*a.sp*) immediately in front, of the level of the posterior dorsal spine (*pd.sp*). There are two pairs of well-developed intermediate spines (*isp1*, *isp2*), with the anterior pair inserted between the pectoral spines (*p.sp*). There are neither median nor paired prepectoral spines, and no dermal plates in the shoulder-girdle.

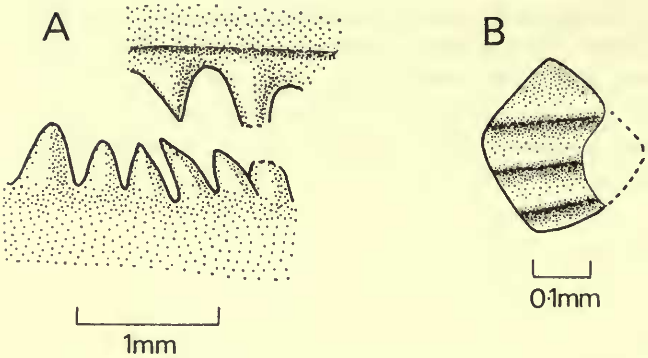
Table 2

Length (in millimetres) of exserted portion of fin-spines of *Uraniacanthus spinosus* gen. et sp. nov.

Specimen	Ant. dorsal	Post. dorsal	Pectoral	Pelvic	Anal
P.16609	24	14	—	12	15
P.16610–1	—	21	—	11	20
P.16612–3	—	—	Ca. 16	—	—
P.20000–1	—	28	—	—	33
P.53030–1	—	24	—	12	—
P.53032–5	32	—	—	—	—

(ii) *Squamation.* The small trunk scales are poorly seen in the specimens. They have a flat base and a moderately high, flat crown. The surface appears to be ornamented with three or four parallel or subparallel ridges, but the restoration in Text-fig. 17B is intended to show only the general character of the crown and it requires corroboration. There is little region variation, and there are no tesserae on the head. The scale crowns are, however, enlarged and further flattened mesial to the base of the pectoral fin, between the pectoral and first intermediate spines, at the bases of some of the other spines (e.g., the posterior dorsal, Pl. 12), and anterior to the first dorsal spine. The number of ridges increases to five or six on these enlarged crowns.

The webs of the median and paired fins are coated with rows of minute scales, and are unusually well preserved (*ad.f*, *pd.f*, *pv.f*, Pls. 11–13). There are no fin webs behind the intermediate spines. The caudal fin (Pls. 11, 12; Text-fig. 18) has scale zone 1 (*Z1*) distinctly developed in the usual way. Zone 2 (*Z2*) is also well differ-



Text-fig. 17. *Uraniacanthus spinosus* gen. et sp. nov. Lower Old Red Sandstone. A, upper and lower teeth from anterior region of jaws. Sketch of BM P.53032. B, sketch of crown of flank scale. After BM P.16613.

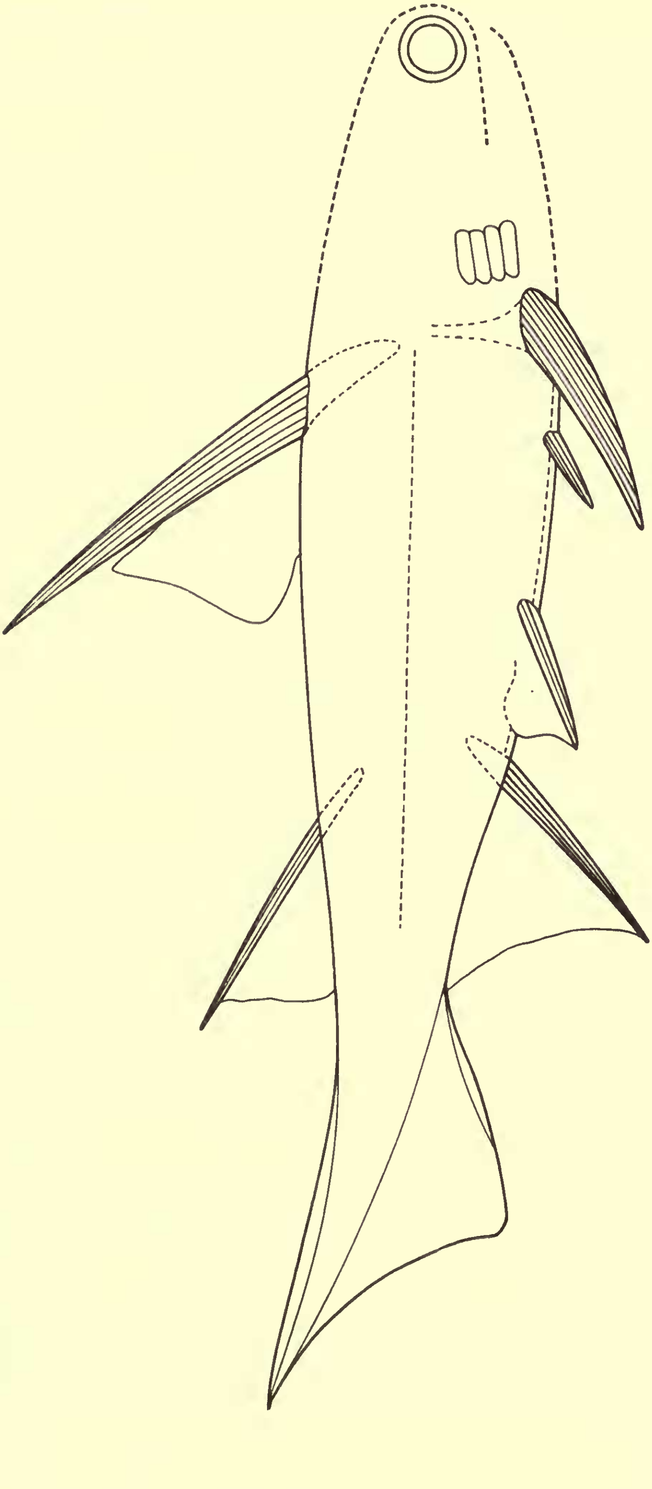
entiated, but as in *Ptomacanthus* it is not clearly subdivided into zones 2 and 2″. Enlarged scales along the margin of the fin may, however, represent zone 2″. The hypochordal lobe bears long rows of fine scales, comparable with those on the dorsal and anal fins (Pl. 12). They cannot be separated into zones 3 and 4, but a narrow band of enlarged scales along the leading edge of this lobe (Pl. 11) is comparable with zone 3″ of *Ptomacanthus*.

The main lateral-line can be observed to pass back between rows of flank scales in P.53030–1; and the ventral line can be seen in P.53035 running between rows of slightly enlarged scales mesial to the pectoral fin. The two lines are restored in Text-fig. 18 on the evidence of these specimens.

(iii) *Spines*. The median fin-spines are deeply inserted in the body muscles (Text-fig. 18, Pls. 11, 12), as they are in *Ischnacanthus gracilis* (Egerton) (Watson 1937, Text-fig. 10). The spines are devoid of nodes, except at the bases of the pectoral and anterior dorsal spines, and can thus be separated immediately from the spines of the other Wayne Herbert species. The number of smooth ridges at each side of the fin-spines near their bases is as follows: anterior dorsal, 8; posterior dorsal, 3 or 4; pectoral, about 8; pelvic, 6; anal, 4 or 5.

(iv) *Shoulder-girdle*. This is represented only by a perichondral scapular ossification (*sc*, Pl. 13, fig. 1; also P.53034), which is similar in its size and relations to that of *Ischnacanthus gracilis* (Text-fig. 18). The lack of dermal bones and prepectoral spines is a further notable difference between *U. spinosus* and the other Wayne Herbert species.

(v) *Head*. The squamation of the body continues forwards on to the head, with little change in character. Four spathiform branchiostegal rays are preserved in P.16612–3 (*br*, Pl. 13). They have an ornamentation of fine, subparallel and partly interconnected ridges. There are probably traces of the circumorbital ring in the same specimen. The jaw remains in P.53032 (Pl. 12, fig. 1) indicate that the palato-



TEXT-FIG. 18. *Uraniacanthus spinosus* gen. et sp. nov. Lower Old Red Sandstone. Restoration in lateral view.

quadrate was low with an extrapalatoquadrate ridge, and that the meckelian cartilage had a deep fossa for the adductor muscles. They show no other details of the replacement bones, but the structures that are preserved are comparable with the corresponding regions of *Ischnacanthus gracilis*. Along the upper margin of the lower jaw, and anteriorly in the upper jaw (Text-fig. 17A), there are preserved single series of teeth firmly anchylosed to the adjacent bones. Each tooth is circular in section and without side cusps. A dental element is also seen in P.16612–3 (*dg.b*, Pl. 13); although it is small, displaced, and the details of its structure are indistinct, it is provisionally determined as a marginal jaw element showing three or four principal cusps and several rows of side-cusps. An alternative interpretation, in which I have almost equal confidence, is that it is a symphysial tooth similar to those figured for *Gomphonchus* (e.g. Gross 1957, Pl. 2). There is no sign of a dermal mandibular bone (i.e. a 'mandibular splint').

A more detailed description and discussion of these jaw elements is not warranted by their preservation. They are important, nevertheless, in establishing that *U. spinosus* is a tooth-bearing fish and that some of the teeth are fused into jaw bones.

Discussion. The presence of tall, deeply inserted dorsal fin-spines, and two pairs of well-developed intermediate spines gives *Uraniacanthus* a superficial resemblance to diplacanthoids. Although teeth are not known in this last group, their presence in *Uraniacanthus* does not seriously detract from this resemblance, because they are primitively present in climatiiforms and might reasonably be expected to occur in primitive diplacanthoids. However, *Uraniacanthus* does not have the large scapulocoracoid or the dermal shoulder-girdle plates that characterise diplacanthoids (p. 191). These are important differences, and I think they are sufficient to demonstrate that *Uraniacanthus* does not belong to this group.

Dentigerous jaw bones are found in both primitive climatiids (*Nostolepis*) and in ischnacanthiforms, and in most cases a detailed study is required before a species can be referred to one or other of these groups on the characters of these elements (e.g. Ørvig 1967). Such a study is not possible with the materials of *Uraniacanthus* now at hand, although it may be noted that the circular section of the teeth favours ischnacanthid affinities (Gross 1957 : 35; Ørvig 1967 : 146). If this evidence is allied with the complete lack of dermal structures in the shoulder-girdle, including prepectoral spines, and the deep insertion of the dorsal and anal fin-spines (which would be unusual in a climatioid carrying dentigerous jaw-bones), it seems evident that *Uraniacanthus* is an ischnacanthiform.

The only other articulated ischnacanthiform is *Ischnacanthus gracilis* from the Lower Old Red Sandstone of Scotland. *Uraniacanthus* differs from this species most notably in the presence of intermediate spines and sculptured scale crowns. In both of these characters *Uraniacanthus* is doubtless more primitive than its Scottish relative.

One result of the description of *Uraniacanthus* is that my definition of the order Ischnacanthiformes (Miles 1966 : 166) now needs to be amended. The words 'no intermediate spines' should be removed from this definition, and I feel it is also advisable to omit the following statements, as it is not known how widely they apply within the group; 'and bearing *Poracanthodes*-type scales along some of the cephalic lateral-lines'; 'a large gill-cover covering the whole of the gill-chamber laterally'; 'symphysial tooth whorl in lower jaw and other tooth whorls in the mouth cavity'. Ischnacanthiforms can be described as acanthodians with dentigerous jaw-bones in both the upper and lower jaws, with two dorsal fins, and without dermal plates and prepectoral spines in the shoulder-girdle.

I have provisionally referred *Uraniacanthus* to the Ischnacanthidae (with the same definition as the Order), as this is the only formally recognised family of ischnacanthiforms, and there is insufficient evidence for a proper discussion of the relations of the genus within the order. Ørvig (1967 : 145; cf. Miles 1966 : 166) has excluded *Acanthodopsis* and *Atopacanthus* from the ischnacanthids, but has yet to publish his revised classification. This exclusion is based on jaw structure and it seems a reasonable step; Ørvig's full results are awaited with interest. Finally I have no reason to suppose that *U. spinosus* is conspecific with *Ischnacanthus kingi* White, *I. wickhami* White, *I.* (?) *anglicus* White, *Onchus wheathillensis* White or *'O.' besomensis* White (1961), all from the English Dittonian.

III. THE STRUCTURE OF ACANTHODIAN SHOULDER-GIRDLES

Order ACANTHODIFORMES

Family **ACANTHODIDAE**

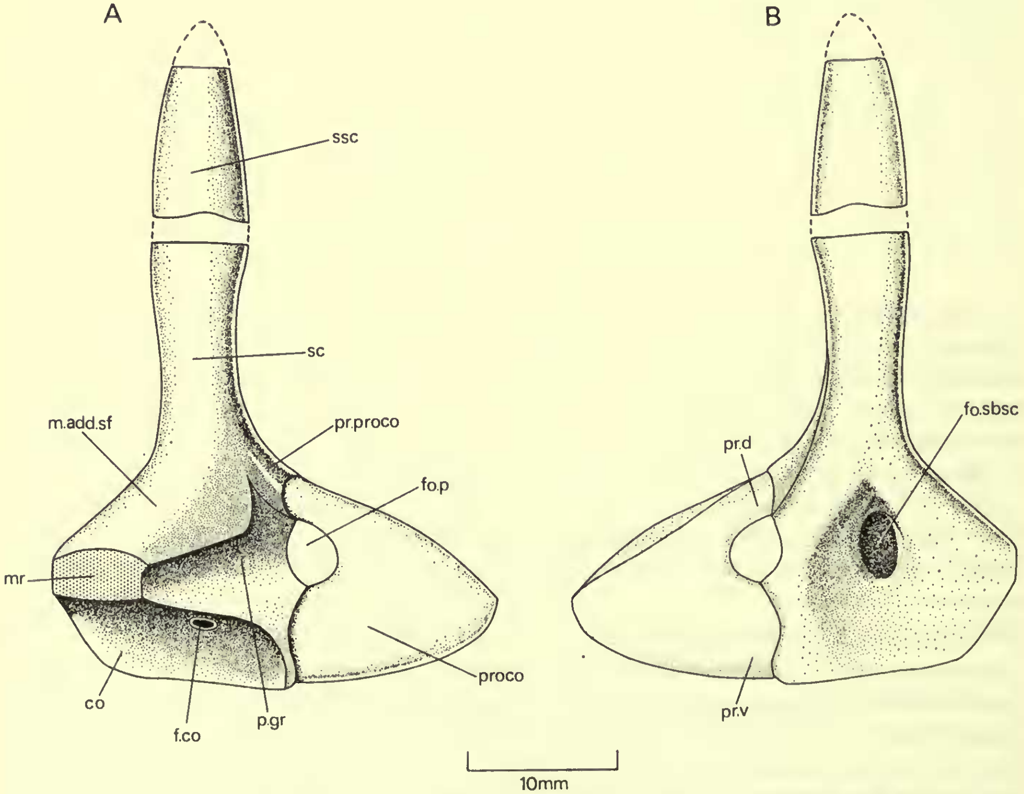
ACANTHODES BRONNI Agassiz

Three authors have described the endoskeletal shoulder-girdle of this species. The first, Reis (1890, Text-fig. 7; 1895, Pl. 6, figs. 11–13), by virtue of his extraordinary interpretation, seems to have gained no clear idea of its structure. The second, Jaekel (1899, Text-fig. 2), produced a brief account which is accurate in most respects, as far as it goes. The third, Watson (1937, Text-figs. 20–22), gave an incomplete account, inferior to the work of Jaekel, to which he did not refer.

The following account, like these earlier works, is based on specimens from the Lower Permian of Lebach, Germany. The negatively prepared specimen in the Berlin collection used by Jaekel is now unfortunately lost, but a cast from this specimen is preserved (HU MB24, copy BM P.49991), and another specimen (HU MB14, cast BM P.49980) confirms all the major points of structure (Pl. 14, figs. 1, 2).

Endoskeletal girdle. The girdle (Text-figs. 19, 20) comprises three separate perichondral ossifications, the scapulocoracoid, suprascapula (*ssc*) and procoracoid (*proco*), which have no contact with their fellows of the other side. The terms suprascapula and procoracoid were applied by Jaekel, and the objection might be raised that it is wrong to use names from bony fishes and tetrapods for ossifications in the girdle of acanthodians. However, terms such as scapula and coracoid have long been applied to ossifications in the primary girdle of different groups of vertebrates without undue confusion, even though these ossifications may not be properly homologous throughout. It is in the same spirit that the terms suprascapula and procoracoid are retained in acanthodians (cf. Dean 1907 : 217). We may orientate the girdle of *Acanthodes* by assuming that the scapular blade (*sc*) stood vertically in the body, and that the procoracoid was directed anteromesially.

The scapulocoracoid has a stout middle region, which is surmounted by a slender scapular blade (*sc*), and is continued ventrally by the coracoid plate (*co*). Posterolaterally the middle region is produced into a horizontal margo radialis (*mr*) for the articulation of the pectoral fin skeleton. Unfortunately the details of this surface cannot be observed. Anteromesially at the same level, the middle region bears a deep groove for the pectoral spine (*p.gr*). The base of the scapular blade descends to the upper edges of the margo radialis and the pectoral spine groove, in a smooth sweep of bone which may be compared with the supraglenoid buttress of primitive



Text-fig. 19. *Acanthodes bronni* Agassiz. Lower Permian. Restoration of shoulder-girdle in A, lateral and B, mesial view. After cast BM P.49991; original from Lebach, Germany.

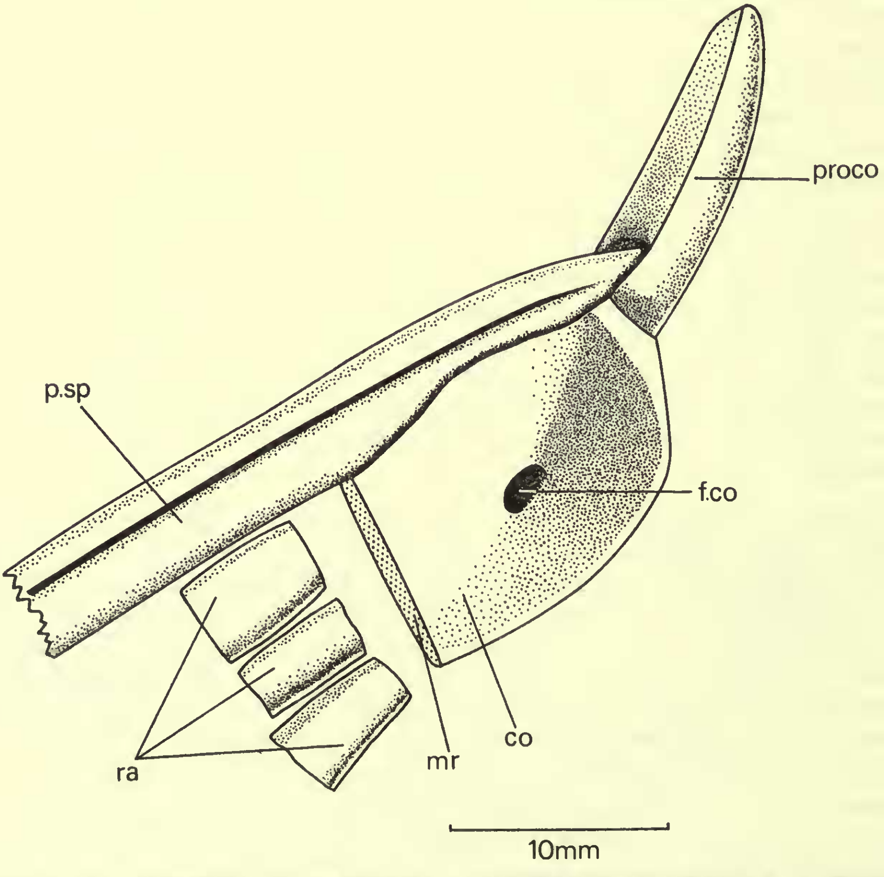
tetrapods and bony fishes (Romer 1924; Andrews & Westoll 1970). The resulting surface (*m.add.sf*) gave origin to the dorsal adductor muscles of the fin. The tip of the scapular blade lacks a perichondral cover, and was presumably connected to the suprascapular by cartilage; the girdle is nearly circular in transverse section at this point (Watson 1937 : 113). Anterolaterally the base of the scapular blade is produced into a procoracoid process (*pr.proco*) over the anterior region of the pectoral spine groove. The terminal face of this process is concave, and lined with endochondral bone.

Below the middle region of the scapulocoracoid, the coracoid plate is hollowed out laterally into an extensive fossa for the origin of the ventral abductor muscles. This fossa is bounded anteriorly by a stout vertical ridge whose anterior face is slightly hollowed into an articular face for the procoracoid. The mesial face of the scapulocoracoid (Text-fig. 19B) is broken by a large subscapular fossa (*fo.sbsc*), which leads to a coracoid foramen (*f.co*) in the ventral muscle fossa. This foramen transmitted diazonal nerves, and possibly blood vessels as well, to the ventral surface of the fin.

The procoracoid (*proco*, Text-figs. 19, 20) is a thin plate standing vertically in the body. The details of its lateral surface are not well known, but probably it lacked prominent features, as does the mesial surface. Posterodorsally it is produced into a narrow process (*pr.d*) of circular cross-section, which articulated against the procoracoid process of the scapulocoracoid; and posteroventrally it is produced into a thicker, deep process (*pr.v*), which abutted against the anterior articular face of the coracoid plate. As a result, superior and inferior articulations may be recognised between the procoracoid and the scapulocoracoid. Between these two articulations, the embayed posterior margin of the procoracoid and the anterior margin of the scapulocoracoid enclose a large pectoral fossa (*fo.p*), which received the head of the pectoral spine (Text-fig. 20). The suprascapula (*ssc*) shows no special features. It lacks perichondral bone both dorsally and ventrally, and was presumably capped with cartilage.

PECTORAL FIN. When the pectoral spine is in place in the groove on the scapulocoracoid, it slopes posterolaterally to enclose an angle of about 60° with the rostrocaudal axis, and inclines ventrally at some 10° from the horizontal. The pectoral fin skeleton of three stout elements which articulate against the margo radialis (*ra*, Text-fig. 20) is well seen in numerous specimens (Pl. 14, figs. 1, 2; Reis 1895, Pl. 6, fig. 11; 1896, Pl. 1, figs. 2, 5, Pl. 2, fig. 4, Pl. 3, fig. 3; Jaekel 1899, fig. 2), and was normally perichondrally ossified (cf. Watson 1937 : 114). A further feature, well seen in many specimens, is the position of the fin-rays ('ceratotrichia', see Miles 1970), which proximally overlie the distal ends of these fin elements.

Watson (1937 : 114, Text-fig. 22) has suggested that there was a second, more distal series of elements in the fin base, and he interprets the endoskeleton as 'tribasal, of general Elasmobranch character', with both basal and radial series, although he finds that 'it is not possible to be sure of the structure'. The photograph of Watson's (1937, Pl. 13, fig. 5) specimen suggests, however, that his 'radial' could be a proximal element of the left fin, whilst his 'pro-', 'meso-' and 'metapterygial' elements are clearly the proximal elements of the right fin. The evidence for Watson's radial series is thus poor, and is not corroborated by other specimens. I suggest, therefore, that the contact between the proximal ends of the fin-rays and the three endoskeletal elements indicates the absence in life of an extensive distal series of elements of the type reconstructed by Watson, and that the three ossified elements of the fin should properly be interpreted as radials. It is of course possible that there was a second short series of radials, unossified, such as found in *Pteronisculus* (Nielsen 1942, Text-fig. 51) and *Acipenser* (Jessen 1968, Text-fig. 8B). If the equivalent of a basal series is to be sought in *Acanthodes*, it may best be looked for as an undifferentiated area in the region of the scapulocoracoid that carries the margo radialis. Like the basal series of primitive elasmobranchs, this region is situated



Text-fig. 20. *Acanthodes bronni* Agassiz. Lower Permian. Restoration of shoulder-girdle and pectoral fin skeleton in ventral view. After cast BM P.49991; original from Lebach, Germany.

proximally to the radials and is in the body wall (cf. *arthrodires*, Miles & Westoll 1968 : 444–445).

Thus the pectoral fin of *Acanthodes* had an articulation with the scapulocoracoid of moderate length; it had a small muscular lobe with three stout, ossified radials; it was aplesodic (Jarvik 1959 : 14); and it had an extensive web which was stiffened with a dorsal and a ventral series of fin-rays. These fin-rays have been described by Watson (1937 : 114). They were usually ossified only most proximally, although there is evidence from the most favourably preserved specimens that they extended to the edge of the fin. Watson notes that each series of 'ceratotrichia' may be folded on itself in laterally compressed specimens, and suggests that this indicates that 'the inner margin of the fin was attached to the body near the ventral surface for a long distance'. But this conclusion conflicts with the evidence from the moderate length of the fin articulation, and it is more likely that the condition results from the ventral deflection of the mesial region of the web, as seen, for example, in sharks and *Acipenser* (Jarvik 1965 : 161, Text-figs. 4A, B, 5E, 8D). Finally, in some specimens, the base of the fin was covered by small scales with a radial arrangement (Watson 1937 : 114), although this condition is better seen in some geologically older acanthodians (e.g. Pl. 15, fig. 1).

Watson (1937 : 114) records that 'the fin spines can be erected so that the two make an angle of 130° with one another'. This is substantiated by the new results presented above, particularly by the moveable joints between the procoracoid and scapulocoracoid. It is still not clear, however, whether the spine was lifted out of the groove, or whether the scapulocoracoid rotated in the body. The second mechanism would explain the cylindrical form of the scapula and the joint with the procoracoid, but would be unusual in comparison with modern fishes (sturgeons, catfishes). There is, however, no evidence of muscles specially developed to move the spine, which might have inserted on the procoracoid, and it is unlikely that muscles inserted directly on the smooth surface of the spine itself. In sturgeons, the pectoral spine (fused lepidotrichia) is attached to the first radial, which articulates with the girdle (Goodrich 1909 : 319, Text-fig. 279). Although there is no indication that the spine was attached to the first radial in *Acanthodes*, it seems likely that it was pushed forward by the fin. Thus it was erected as the web was spread by the operation of anterior erector slips of the dorsal and ventral fin muscles (with antagonistic posterior slips), originating on the scapulocoracoid (or on the procoracoid if the scapulocoracoid rotated with the spine). There is no sign of a mechanism to lock the spine in the erect position (see p. 207).

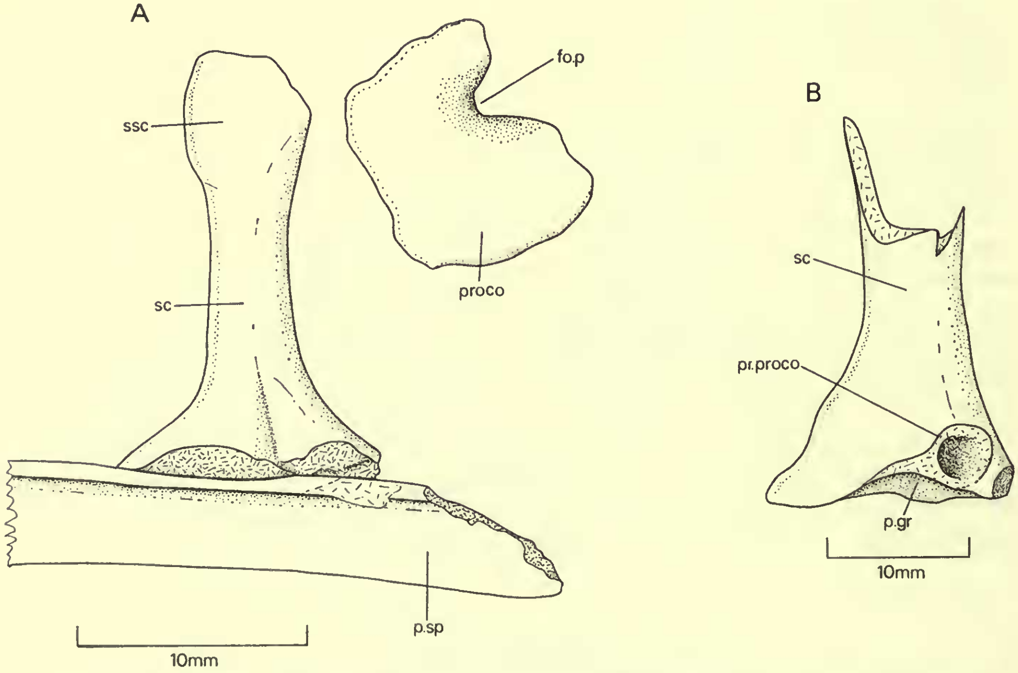
Acanthodes spp.

Certain other species of *Acanthodes* can be shown to resemble *A. bronni* closely in the structure of the pectoral girdle and fin, and this is presumably true of all properly determined species of the genus.

Fritsch (1895, Text-figs. 261, 263, 270) has figured a possible procoracoid ('Infraclavicula') in contact with a scapula ('Clavicula') of unexceptional form in the Lower Permian species *A. gracilis* (Beyrich). The shape of the procoracoid in his drawings suggests, however, some misinterpretation of the specimens.

Davis (1894 : 255, pl. 28, figs. 4, 5) has figured the scapula in the Upper Carboniferous *A. wardi* Egerton, and shown that it bears the same relationship to the pectoral spine as in *A. bronni*. One of his specimens (Text-fig. 21A) shows the procoracoid (*proco*), which is apparently closer in structure to that of *A. bronni* than is the procoracoid of *A. gracilis*. The swollen top of the scapulocoracoid in this specimen indicates that the suprascapula (*ssc*) is co-ossified with the scapular blade (*sc*). The similarities to *A. bronni* are confirmed and extended by another right scapula of *A. wardi* (Text-fig. 21B), which exhibits a distinct procoracoid process (*pr.proco*) and the upper part of the pectoral fin-spine groove (*p.gr*).

Since the above was written, Mr Steen R. Jensen (Copenhagen) has drawn my attention to the procoracoid of *A. nitidus* Woodward, from the Calciferous Sandstone Measures of Glencartholm, Scotland (BM P.20438). This element and the associated scapular blade have the expected form for a species of *Acanthodes*.



Text-fig. 21. *Acanthodes wardi* Egerton. Upper Carboniferous. A, sketch of shoulder-girdle, BM P.8058, Knowles Ironstone Shale, Fenton, Staffordshire, England. B, sketch of scapula, BM P.8435, Upper Coal Measures, Collyhurst, Bradford, nr. Manchester, England.

Family **CHEIRACANTHIDAE**

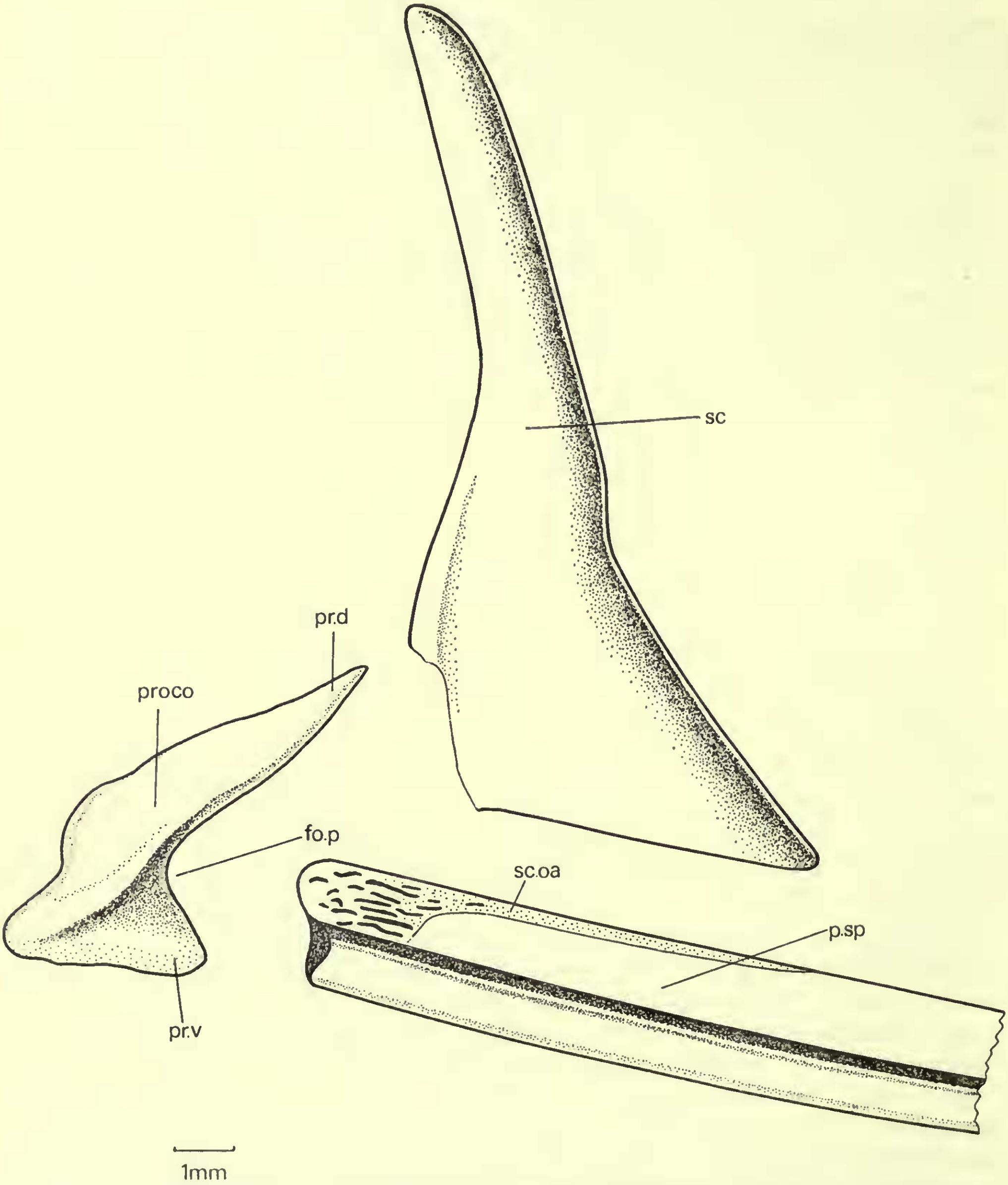
Cheiracanthus spp.

This account is based on specimens of *Cheiracanthus latus* Egerton and *C. murchisoni* Agassiz from the Moray Firth nodule beds in the Middle Old Red Sandstone of Scotland. Scores of specimens are preserved in the BM and the RSM. Watson (1937 : 84) remarks that these species 'are identical in their morphology but differ in proportions and in some details'. I am not sure that this is true with respect to the gill-covers, but the shoulder-girdles are closely similar in structure.

Endoskeletal girdle. The shoulder-girdle is well seen in specimens of *C. latus*, notably BM 34052, 36010 and RSM 1877.30.2 (also *Cheiracanthus* sp., RSM 1968.19.18 and RSM Kinnaird 168). The scapular region is perichondrally ossified except in its anteroventral corner, but there is no sign of the middle and coracoid plate regions, which must have been cartilaginous (Text-fig. 22, Pl. 15, fig. 2). The scapular blade (*sc*) apparently leaned slightly forwards in the body (Watson 1937, Text-figs. 12, 13) and has a circular cross-section. It includes the separate suprascapular of *Acanthodes bronni*. Ventrally the scapular blade is plate-like, and its outer surface ends in an almost straight lower edge which was in contact with the pectoral spine (*p.sp*). Thus it formed the upper border of a pectoral spine groove. The region in which one might expect to see the procoracoid process is not ossified, so it is not known whether this structure was present, although the form of the surrounding regions of the scapula suggest that it was. There is no indication of the margo radialis, and the mesial face of the scapula shows no important features, except in BM 36010 where it appears to include the upper part of a small subscapular fossa.

The procoracoid (*proco*) is a thin, vertically standing plate of perichondral bone ('coracoid', Watson 1937), closely comparable with that of *Acanthodes*. It is provided with a posterodorsal (*pr.d*) and a posteroventral (*pr.v*) process for superior and inferior articulation with the scapulocoracoid, but the nature of these articulations and the exact orientation of the element cannot be determined. Between these processes the posterior margin is embayed, which indicates the existence of a pectoral fossa (*fo.p*) for the head of the pectoral spine. The lateral face is marked by an oblique ridge and a slight depression in front of the posterior embayment.

Pectoral fin. The dermal pectoral spine is well known (Watson 1937). Proximally its leading face is marked by a narrow dorsal area (*sc.oa*, Text-fig. 22) which was overlain by the lower edge of the scapular ossification. This area gives way to a more coarsely textured area which was deeply inserted in the body wall. The relationship of the spine to the scapulocoracoid and its orientation in the body seem to have been very much as in *Acanthodes*, although the spine was probably less mobile than in this genus. Watson (1937) apparently erred in showing the spine detached from the scapula in his reconstruction. The endoskeleton of the fin is unknown, but the disposition of the fin-rays indicates that there was a small muscular lobe with short radials. The 'ceratotrichia' are particularly well seen in a specimen of *C. murchisoni* (Pl. 20, fig. 2). They are long, slender, unjointed rods in separate dorsal and ventral series, which reach well out towards the margins of the extensive web. They compare well with the 'ceratotrichia' of *Ischnacanthus gracilis* (Egerton) (Miles 1970, Text-fig. 8).



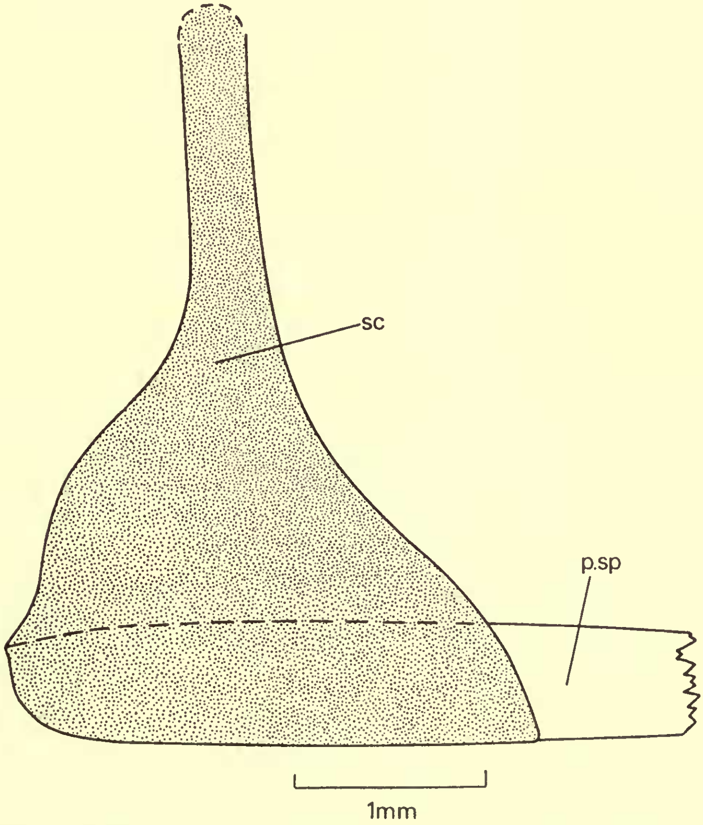
TEXT-FIG. 22. *Cheiracanthus latus* Egerton. Middle Old Red Sandstone. Restoration of shoulder-girdle with bones shown slightly apart, in lateral view. Mainly after BM 35052, Tynet Burn, Banffshire, Scotland.

Family MESACANTHIDAE

Mesacanthus mitchelli (Egerton)

The shoulder-girdle and pectoral spine can be seen in many specimens from the Lower Old Red Sandstone of Angus, Scotland. I have examined the collections in the British Museum (Nat. Hist.) and the Royal Scottish Museum. Unfortunately the shoulder-girdle is usually poorly preserved, and in some respects it is difficult to interpret.

ENDOSKELETAL GIRDLE. Watson (1937 : 76, Text-figs. 8, 9) has described the salient features and it is only necessary to discuss some points which are open to a new interpretation. The following remarks are based mostly on BM 38594, P.7002 and P.1331. The perichondrally ossified girdle comprises the scapular blade (*sc*) and part of the middle region. The ossification spreads down inside the admesial



TEXT-FIG. 23. *Mesacanthus mitchelli* (Egerton). Lower Old Red Sandstone. Restoration of shoulder-girdle, in mesial view. After BM 38594, P.1331, P.7002, Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

face of the pectoral spine (Text-fig. 23). It is likely, therefore, that the spine was lodged in a groove on the outer face of the scapulocoracoid, although this cannot be confirmed with the specimens at hand. Watson records that the 'lower part of the bone has an ornamented surface as if it had a series of large overlapping scales fused on to it'. However, this 'ornamentation' is found on both the lateral and mesial surfaces and seems to be the result of post-mortem changes in the perichondral bone; it has a quite different appearance from the ornamented dermal bone found in the shoulder-girdle of contemporary climatiiform acanthodians. It is, therefore, not evident that dermal bone is included in the make-up of the girdle in *Mesacanthus*, and it seems unlikely that the surface of the girdle was exposed on the flank as Watson supposed. The scapula shows no sign of a procoracoid process. This may be due to poor preservation, but it seems more likely that this structure was absent. A procoracoid ossification has also not been recorded. This may be because (1) it has not been recognised in the specimens; (2) it was a separate element but is not ossified; (3) it was included in (co-ossified with) the scapulocoracoid, and therefore had no separate existence. It seems that explanation (2) or (3) is likely to be correct, but there is not yet enough evidence to decide between them. Nothing is known of the margo radialis.

PECTORAL FIN. It is unnecessary to add to earlier descriptions of the fin-spine, and the skeleton of the fin is not preserved.

Order ISCHNACANTHIFORMES

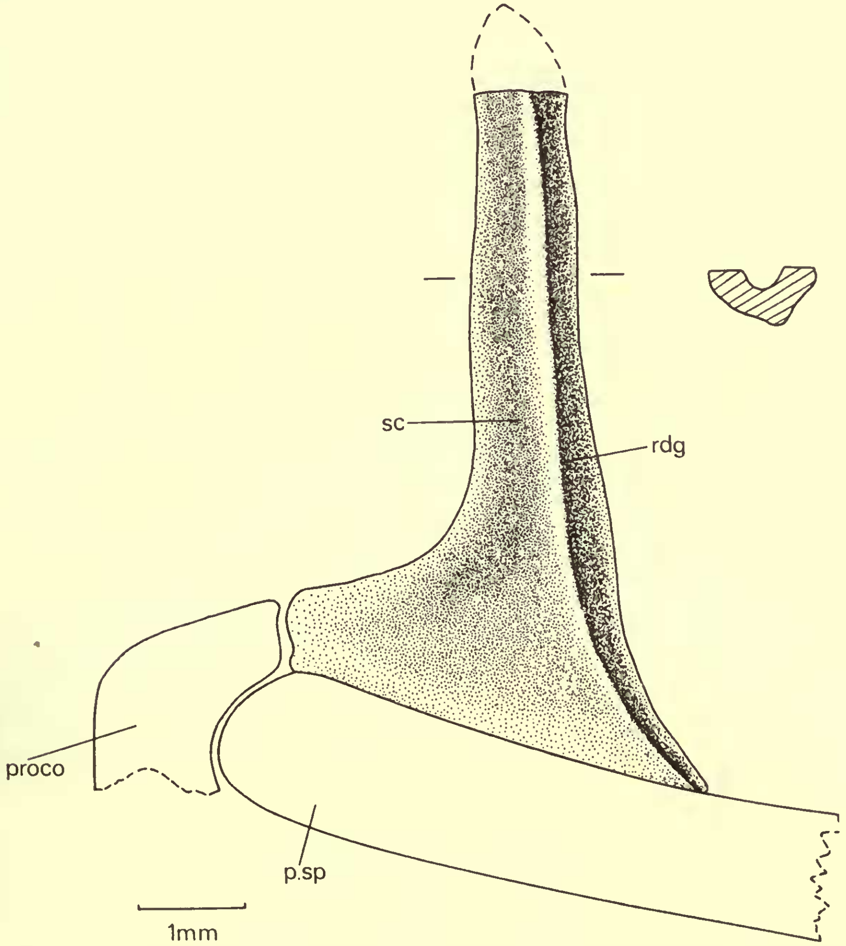
Family **ISCHNACANTHIDAE**

Ischnacanthus gracilis (Egerton)

I. gracilis is the only ischnacanthiform in which the pectoral fin and shoulder-girdle are adequately known. It is represented by many specimens from the Lower Old Red Sandstone of Scotland, and I have examined the large collections in the BM and the RSM. Unfortunately, as in the case of *Mesacanthus mitchelli* from the same beds, the details of the girdle and fin are difficult to interpret with any degree of certainty.

ENDOSKELETAL GIRDLE. The shoulder-girdle (Text-fig. 24) is represented by a scapular ossification (*sc*) of about the same extent as in *Mesacanthus*, although its mesial wall is incompletely ossified. Watson's (1937, Text-figs. 10, 11) drawings of this structure are accurate and he shows it in its correct relationship to the pectoral spine. However, he incorrectly concluded that it was partly dermal in origin, and this led him to the further incorrect conclusion that its inner face lay in contact with a cartilaginous scapula. To my mind there can be no doubt that the structure preserved in the fossils is of perichondral origin, and therefore properly termed the scapula. This is supported by two observations made by Watson (1937 : 81): (1) this structure was covered by ordinary body scales, (2) it is devoid of ornamentation.

The outer surface of the scapula (Text-fig. 24) is angled, so that it presents antero- and posterolateral faces which are sometimes separated by a low ridge (*rdg*). The anterolateral face may have formed a posterior wall to the gill-chamber, whilst the posterolateral face seems to have descended to a well-formed margo radialis. Several specimens (e.g. BM 46305c, d) give evidence of an incompletely ossified procoracoid (*proco*, Text-fig. 24). This element is closely comparable with the procoracoid of acanthodiforms, and appears to have had similar relations to the pectoral spine and scapula. However, as in the case of *Cheiracanthus*, there is no sign of a procoracoid process of the scapula.



TEXT-FIG. 24. *Ischnacanthus gracilis* (Egerton). Lower Old Red Sandstone. Restoration of shoulder-girdle in lateral view. After RSM Mitchell collection 86; BM P.9203, 46305c, d. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

Pectoral fin. Watson recorded the presence of four endoskeletal elements in the pectoral fin (RSM 1891.92.258). These may now be interpreted as radials by comparison with *Acanthodes bronni*. As in this last species, the 'ceratotrichia' radiate from the distal ends of these elements. These fin-rays have recently been redescribed (Miles 1970, Text-fig. 8). BM P.9118 shows that the web of the fin was coated with small scales running in long, radiating rows.

Order CLIMATIIFORMES

The shoulder-girdle of climatiiforms is characterised by the possession of ventral dermal plates. These plates are probably not homologous with the bones of the osteichthyan shoulder-girdle (see p. 205), although they may occupy more or less the positions of the cleithrum, the clavicle and the interclavicle. Hitherto a series of simple topographical names has been applied to them, such as 'anterior lateral plate', 'median ventral plate' and 'ventrolateral plate' (Watson 1937; Ørvig 1967). Unfortunately this terminology has not always been used accurately, and for my purposes it has proved to be inadequate for a proper discussion of the structure and evolution of the girdle. Another disadvantage is that it is similar to the terminology applied to the plates of the trunk-shield in placoderms, in which group acanthodians have been classified (e.g. Moy-Thomas 1939), although these fishes are no longer thought to be closely related (Miles 1965). There is little possibility that the dermal plates of acanthodians and placoderms are homologous. For these reasons I have found it necessary to introduce a new terminology for the plates in acanthodians, and this is done in the account of *Climatius reticulatus*. The compound plate names used in the descriptions of some species should be taken to imply (necessarily somewhat vague) topographic correspondence only. It is not possible to use a more precise terminology, based securely on the evolution of the plates, because there is no evidence to reveal with any certainty the primitive condition of the climatioid girdle (pp. 195–200).

Dean (1907 : 215) has asserted that the fins of acanthodians are 'beyond peradventure of a lateral fin-fold type', and this view has persisted to the present day to find expression most recently in the terminology applied by Ørvig (1967) to the prepectoral spines. Despite Dean's assertion, it seems that the fin-fold theory in its more naïve form has nothing to contribute to the study of acanthodians (Westoll 1958; Miles 1970 : 356), and this view is reflected in the terminology given below to the spines.

Suborder CLIMATIOIDEI

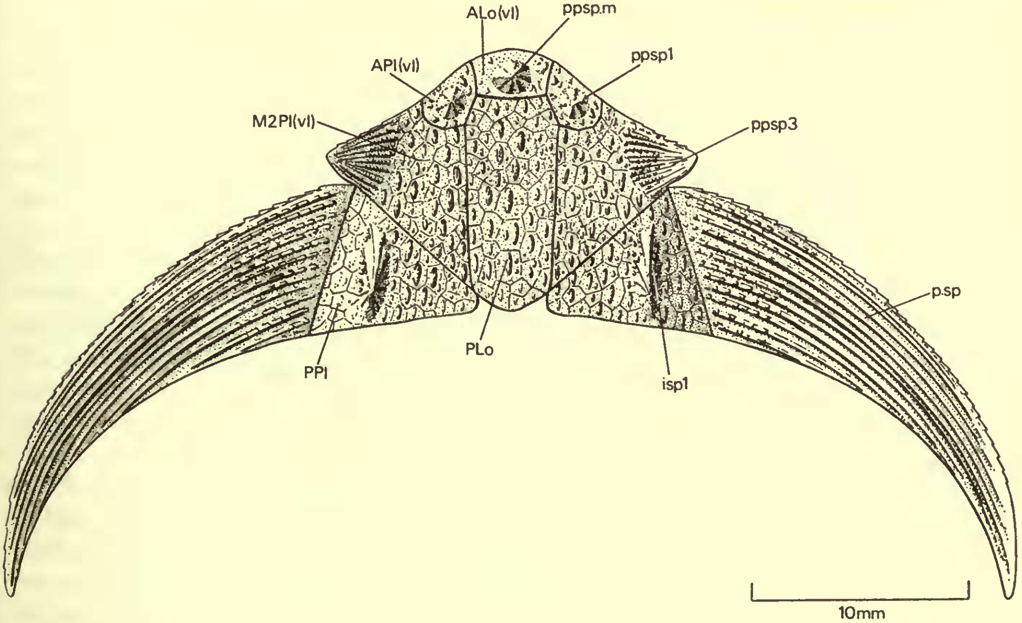
Family **CLIMATIIDAE**

Climatius reticulatus Agassiz

The shoulder-girdle of this species was first described by Watson (1937), and later by Ørvig (1967) who corrected a number of serious mistakes in the original account.

However, a fully accurate description remains to be given. The following account is based on specimens in the British Museum (Nat. Hist.), the Royal Scottish Museum and GSM 49785, all from the Lower Old Red Sandstone of Scotland.

Dermal skeleton. The dermal plates are in two series (Text-figs. 25, 26), a paired lateral series of three pinnal plates (*APl, M2Pl, PPl*) and a median series of two lorical plates (*ALo, PLo*). All but the posterior lorical plate are related to a spine of the intermediate-prepectoral series, and lateral to this spine series lies the pectoral spine (*p.sp*), which is attached to the posterior pinnal plate. Watson's (1937 : 60) account speaks of 'an area of tightly interlocked small bones' mesial to the base of the pectoral spine, whilst Ørvig (1967 : 137) affirms that the plates in this region are ornamented bones. The true condition of the dermal skeleton is clearly revealed by a number of specimens (Pls 3, 16, fig. 2), which show that the major plates of the girdle are thin, deeply-seated laminae of bone, and that these are overlain by mosaics of small polygonal scale-like bones. It seems probable that the plates comprise the fused basal layers of scales, and that the small bones are the free crowns of these scales (p. 198; cf. *Nostolepis*, Gross 1971), although the presence of entire, discrete scales is a preclimatioid condition. The ornamentation of the plates and spines is shown in the photographs (also Ørvig 1967) and will not be described further. The mutual relations of the spines and plates can be seen in the restorations (Text-figs. 10, 25, 26).



Text-fig. 25. *Climatius reticulatus* Agassiz. Lower Old Red Sandstone. Restoration of shoulder-girdle in ventral view. After RSM 1887.35.5B, 1963.2.5; BM P.6964, P.1343a, 38596. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

The anterior lorical plate (*ALo*, 'median dermal bone', Watson 1937) has a ventral spine-bearing lamina (*vl*) and an ascending lamina (*al*) which rises for a short distance in the hind wall of the gill-chamber. Both laminae are arched, and they merge smoothly with each other so that the plate is hemicylindrical in cross-section. The plate shows no sign of subdivision into scales and it was not recognised as a structure distinct from the spine by Ørvig (1967). The last element may be termed the median prepectoral spine (*ppsp.m*; 'unpaired median prepectoral fin-fold spine', Ørvig 1967); it is open basally on the visceral surface of the plate (*cav.sp*, Text-fig. 26B). The posterior lorical plate (*PLo*; 'median ventral plate', Ørvig 1967) is probably the structure misinterpreted as a paired 'anterior admedian' by Watson (1937: 60; cf. Ørvig 1967 : 139). It is slightly too narrow in Ørvig's restoration, but is otherwise correctly placed. Unlike the anterior lorical it is overlain by scale-like plates. It is only necessary to add that the visceral surface exhibits an extensive, shallow pericardial depression (*dp.pc*).

The anterior pinnal plate (*APl*) was reasonably described as a 'cylindrical dermal bone' by Watson (1937 : 60), but was not distinguished from its spine by Ørvig (1967). Like the anterior lorical plate it has a ventral spine-bearing lamina (*vl*) and an ascending lamina (*al*). The margins are difficult to fix but it appears that the surface shows no subdivision into scale-like areas (Pl. 16, fig. 2). The spine is ventrally directed, and it may be termed paired prepectoral spine 1 (*ppsp1*; 'paired prepectoral fin-fold spine', Ørvig 1967); its cavity opens on the visceral surface of the plate.

The remaining pinnal plates are covered with scale-like elements. The middle pinnal (*M2Pl*, 'anterior lateral plate', Watson 1937; 'first ventrolateral plate', Ørvig 1967) again comprises ventral and ascending laminae, and at their junction arises a short, ventrolaterally directed spine. Because of the number of paired prepectoral spines in *Erriwacanthus falcatus* Ørvig (Text-fig. 27), this is here termed paired prepectoral spine 3 (*ppsp3*) and the plate is more correctly termed the second middle pinnal plate. Paired prepectoral spine 2 is held to be absent in *Climatius reticulatus*.[3] The cavity of the spine opens on the visceral surface in the angle between the two laminae. The posterior pinnal plate (*PPl*; 'second ventrolateral plate', Ørvig 1967) is more or less triangular and has no ascending lamina. Laterally it is firmly attached to the pectoral spine (*p.sp*), but whether in a butt joint or with an overlapping suture is not known (cf. *Diplacanthus*, p. 191). A short, ventrally-directed spine arises from its surface (*i.spl*; 'ridged dermal bone', Watson 1937; 'fin-fold spine of the ventro-lateral plate', Ørvig 1967). I now regard this, and its homologue in other climatiiforms, as the first intermediate spine. This differs from my earlier practice with diplacanthids (Miles 1966 : 169, footnote), although in this group Westoll (1958) has already included the spine ('admesial pectoral spine', Watson 1937) in counts of the intermediate series. As indicated above, the prepectoral, intermediate and pelvic spines form a continuous series. The pectoral

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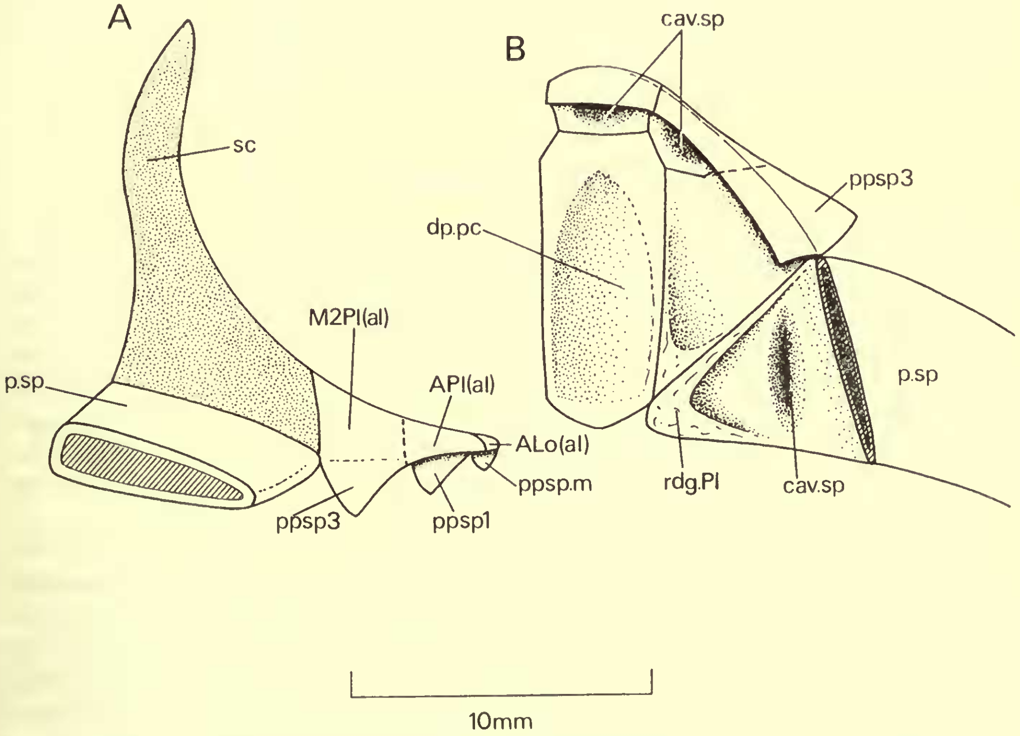
[3] It will be noted in the following accounts that there is some difficulty in determining the prepectoral spines in species in which their numbers have been reduced. The problems of homologising intermediate and prepectoral spines are discussed on p.197.

spine lies lateral to this series (p. 206). The cavity of the first intermediate spine (*cav.sp*) opens on the visceral surface of its supporting dermal plate, exactly like the prepectoral spine. Thus I cannot agree with Ørvig (1967 : 137) that this spine differs from the prepectoral spines in its development. I agree with Ørvig, however, in concluding that Watson's paired 'posterior admedian' plates, between the posterior pinnals, have no real existence. The visceral surface of the posterior pinnal is raised into a low, broad ridge (*rdg.Pl*) around the mesial angle and anteromesial margin of the plate. There is some indication of a similar ridge around the posteromesial angle of the second middle pinnal plate.

ENDOSKELETAL GIRDLE. The ossified endoskeleton (Text-fig. 26) is represented by the perichondral scapula (*sc*), which has been described by Watson (1937 : 60). Its lower lateral margin is firmly attached to the pectoral spine. Unfortunately, the exact extent of the anteroventral region cannot be determined, as here the perichondral bone becomes confused with the lateral laminae of pinnal plates, but it is likely that a coracoid process existed of comparable extent to that of *Ptomacanthus*



TEXT-FIG. 26. *Climatius reticulatus* Agassiz. Lower Old Red Sandstone. Restoration of shoulder-girdle in A, lateral view and B, dorsal view, with left lateral plates omitted. After RSM 1891.92.198, 1887.35.5A, 1963.2.5; BM P.1343, P.6964, P.6964a. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

(Text-fig. 4A) and other genera (Text-figs. 29, 31, 32). Although the coracoid region is unossified, it appears that it sat accurately over the posterior pinnal plate, and it had a broad posterior face which rose to a horizontal margo radialis in the middle region of the scapulocoracoid, mesial to the pectoral spine. The thickened rim of the second middle pinnal plate similarly received the mesial wall of the coracoid process, and the anteromesial ridge of the posterior pinnal received the base of an endochondral septum (p. 172).

A group of body scales is closely applied to the lower part of the lateral surface of the scapula (Pl. 2). This condition is, however, better seen in other genera (e.g. Text-fig. 29A).

Pectoral fin. The pectoral spine is shown in the illustrations, and there is no need to add to earlier descriptions. It is orientated with its proximal end above and its tip well below the base level of the ventral plates. The leading edge is carried slightly below the trailing edge, so that the spine is angled at about 10° to the horizontal.

The only other evidence of the pectoral fin is provided in a few specimens by patches of small scales in the appropriate region (Watson 1937, Pl. 5). These scales are less obviously arranged in rows than in other acanthodians, and are about 1/4 of the size of the adjacent flank scales. They nevertheless show that a well-developed pectoral fin with a sizeable web was present (cf. Westoll 1945 : 382).

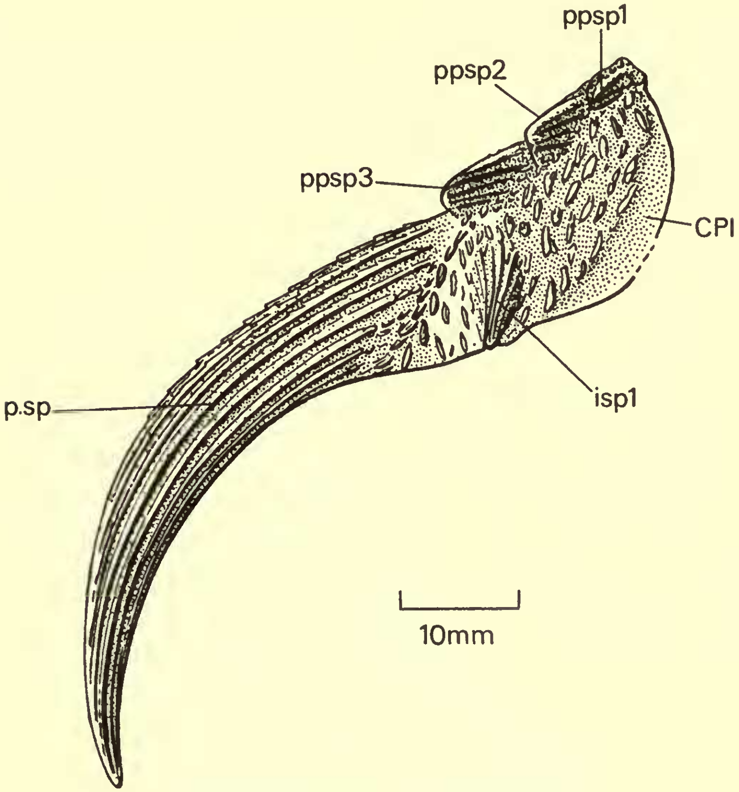
Erriwacanthus falcatus Ørvig

Ørvig (1967) has described under this head the right half of the dermal shoulder-girdle of a climatiid from the Old Red Sandstone of the Ukraine, which is preserved as an intaglio. The specimen (Text-fig. 27) comprises a long pectoral spine attached to an ornamented dermal plate (*CPl*; 'ventrolateral plate'). This plate is transversely arched in its posterolateral corner, so that the pectoral spine (*p.sp*) is carried above the base level. There are three flattened paired prepectoral spines (*ppsp1–3*) on its lateral margin before the pectoral spine, and the first intermediate spine (*isp1*) is attached mesially to the base of the pectoral spine. No sutures can be seen between the spines and the dermal plate, and there is no sign of the subdivision of the superficial layers of the plate into scale-like areas.

The plate may be termed the copinnal plate (*CPl*). It certainly includes the equivalents of the anterior, second middle and posterior pinnal plates of *Climatius reticulatus*. However, it follows from the hypothesis that these plates are each associated with one spine of the prepectoral-intermediate series, that there is an additional first middle pinnal plate component in *Erriwacanthus* associated with paired prepectoral spine 2. This spine (*ppsp2*) may also be present in *Vernicomacanthus* spp. and *Parexus* spp. (Text-figs. 14, 15A).

Whether or not the copinnal plate of *Erriwacanthus* was connected to its antimere by median plates (loricals) is unknown, but it seems probable that it was.

The endoskeletal shoulder-girdle and pectoral fin are unknown.



TEXT-FIG. 27. *Erriwacanthus falcatus* Ørvig. Lower Old Red Sandstone. Right lateral region of shoulder-girdle in ventral view. After Ørvig 1967, Text-fig. 1A and cast BM P.29075. Upper part of Old Red, Dwinogrod, Ukranian SSR.

Erriwacanthus manbrookensis sp. nov.

Pl. 18, fig. 1

1967 *Parexus* sp.; Ørvig : 139, pl. 1, fig. 4

ETYMOLOGY. From Man Brook.

DIAGNOSIS. A species which differs from *E. falcatus* in the disposition of the three paired prepectoral spines, particularly in the wide spacing of prepectoral spines 2 and 3, and in the more lateral position of number 1.

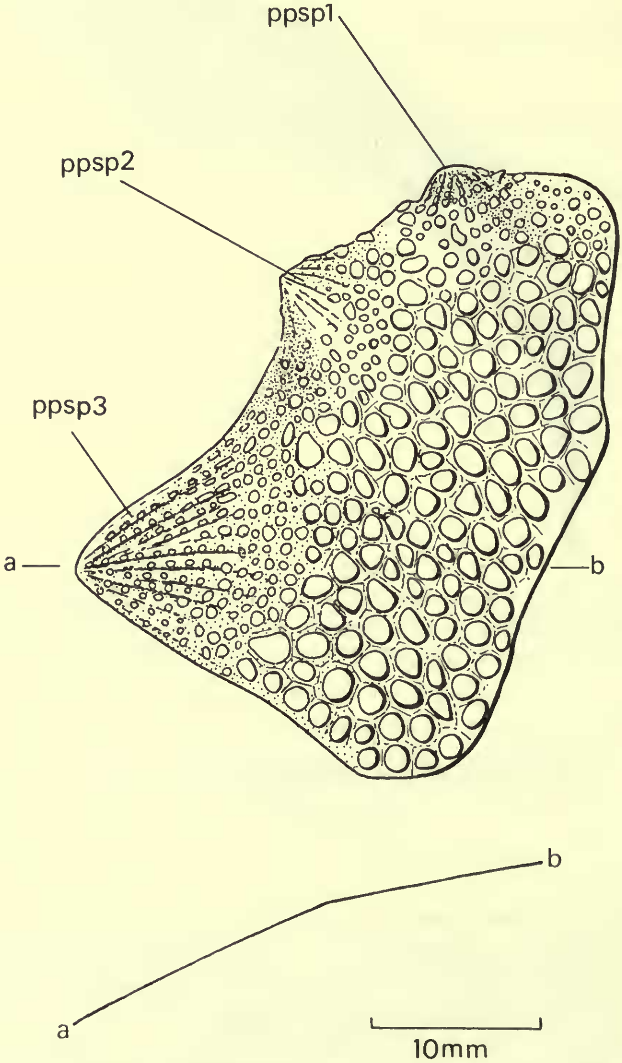
TYPE. The holotype is BM P.20185 (Ørvig 1967, Pl. 1, fig. 4).

HORIZON. Downton Series, Red Marl Group, *Tesseraspis* zone (White 1950; 'stage I.6', King 1934).

LOCALITY. Man Brook 7, Shatterford, near Trimpley, Worcestershire, England.

Material. BM P.20185, P.48984.

Description. Ørvig has figured two conjoined prepectoral spines (P.20185), but a second specimen (P.48984) shows that they are part of a series of three attached to an extensive ascending lamina of a compound pinnal plate (Text-fig. 28, Pl. 18, fig. 1). The ventral lamina of this plate and the endoskeletal girdle are still unknown. The ascending lamina is ornamented with large, smooth, low tubercles, which merge



Text-fig. 28. *Erriwacanthus manbrookensis* sp. nov. Lower Old Red Sandstone. Ascending pinnal lamina and paired prepectoral spines in dorsolateral view, with profile a–b of superficial surface. After holotype, BM P.48984. Downton Series, Red Marl Group, Man Brook 7, Shatterford, Worcestershire, England.

almost abruptly with those situated on the ridges of the prepectoral spines. The ascending lamina shows no sign of subdivision into component pinnal plates. However, it is superficially subdivided into many small polygonal tesserae each with a single tubercle at its centre. The skeleton is thus comparable with the ventral plates of *Climatius reticulatus*, in the division of the superficial layer into scale-like areas which are attached to one or more large sheets of basal bone. The paired prepectoral spines are set at varying angles. Number 3 (*ppsp3*) projects ventrolaterally at some 15° away from the plane of the ascending lamina; number 2 (*ppsp2*) projects laterally in the plane of the lamina; and number 1 (*ppsp1*) also projects laterally, but is more prominently placed on the surface of the lamina than is number 2.

REMARKS. *Erriwacanthus manbrookensis* can be shown to resemble *E. falcatus* in only one character, the presence of three paired prepectoral spines. This may be the primitive number for climatioids (p. 196), and if so it is not good evidence that these species are congeners. However, there is neither evidence to relate *E. manbrookensis* to any other named genus, nor sufficient information to define or warrant the erection of a new genus. For these reasons the species is provisionally referred to *Erriwacanthus*. It differs from *Parexus* spp. in the presence of an extra paired prepectoral spine, presumably in the composition of the compound pinnal plate, and in its more extensive ascending lamina. Although the matter is not discussed by Ørvig (1967), it seems unlikely that these shoulder-girdle remains are conspecific with the spine described by Traquair (1894b, '*Parexus*') from the base of the Ditton Series (Cradley) in Herefordshire.

SABRINACANTHUS gen. nov.

ETYMOLOGY. L. *sabrina*, the River Severn; Gr. *akantha*, a thorn.

DIAGNOSIS. A climatiid with extensive, ornamented ventral and ascending pinnal laminae, which differs from *Erriwacanthus* and *Brachyacanthus* in the absence of paired prepectoral spine 1, and from *Climatius*, *Ptomacanthus* and *Brachyacanthus* in the presence of paired prepectoral spine 2; scapular blade with a slender dorsal shank.

TYPE SPECIES. *Onchus arcuatus* Agassiz 1837.

Sabrinacanthus arcuatus (Agassiz)

Pl. 17

1837 *Onchus arcuatus;* Agassiz : 7
1843 *Onchus arcuatus;* Agassiz, Pl. 1, figs 3–5
1844 *Byssacanthus arcuatus;* Agassiz : 111
1967 '*Onchus*' *arcuatus;* Ørvig : 140, text-fig. 3
1967 *Erriwacanthus* sp.; Ørvig : 135–136, Pl. 1, fig. 2

DEFINITION. The sole species referred to the genus.

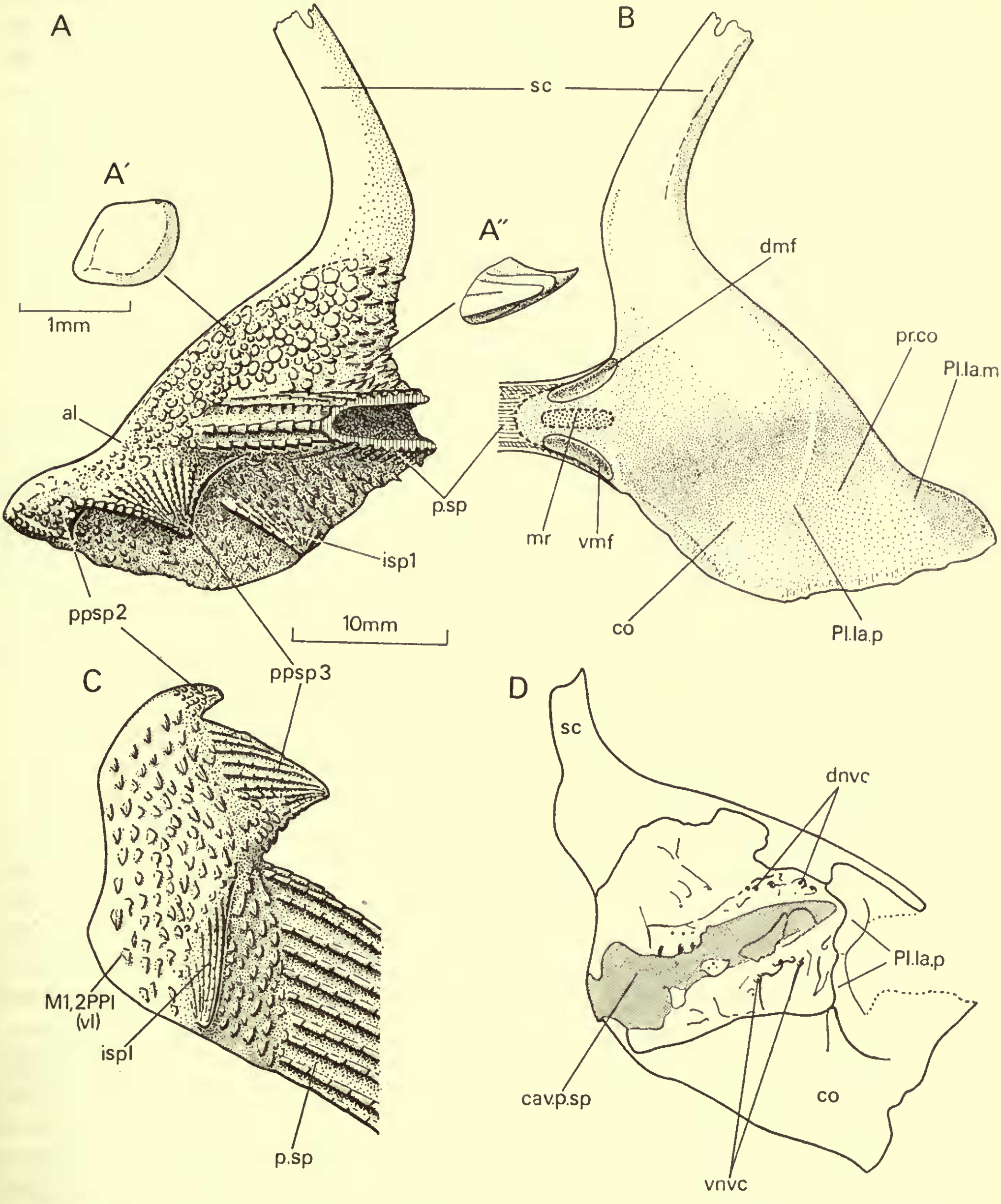
TYPE. Ørvig proposed that the specimen depicted by Agassiz in Pl. 1, fig. 4 (1843) should be the lectotype, but he did not point out that the whereabouts of this specimen are unknown. In fact the specimen may have been lost, together with others in the Murchison collection (Murchison 1853 : 16). A further complication is introduced by the possibility that the shoulder-girdle (UMO D17) figured by Ørvig (1967, Pl. 1, fig. 2) as *Erriwacanthus* sp. is the counterpart of this specimen. The locality of the former is given as Cradley, Herefordshire, and of the latter as Bromyard, but according to the best information now available these might well be the same locality (H. A. Toombs, pers. comm.). The ratios of pectoral spine curvature given by Ørvig for these specimens are remarkably alike, considering that one set is based on an illustration and the other on an incomplete specimen.

The present situation is clearly unsatisfactory, but in view of the possibility that a counterpart exists to the nominal lectotype, I propose to make no changes at this time.

HORIZON AND LOCALITIES. The following account is based on five specimens from the lower part of the Ditton Series, zone of *Pteraspis leathensis*. All are from the right bank of the R. Severn, Nass House, Lydney, Gloucester, England.

MATERIAL. The specimens are as follows: BM P.53120a, b; P.53121a, b; P.53122a, b; P.53123a, b; P.53124a, b. All show articulated parts of the shoulder-girdle. The first specimen has been positively prepared, and the last four have been negatively prepared with diluted hydrochloric acid and studied with the aid of rubber casts (Pl. 17).

DERMAL SKELETON. It is probable that median ventral dermal elements existed, comparable with the loricals of *Climatius reticulatus*, but they have not been preserved. This account is concerned, therefore, with paired lateral plates and their spines. There is a compound pinnal plate (*M1,2PPl*) with a prominent ornamentation on its ventral (*vl*) and ascending (*al*) laminae (Text-fig. 29, Pl. 17, figs. 2, 3). Laterally it gives rise to a pectoral (*p.sp*) and two paired prepectoral spines (*ppsp2*, *ppsp3*). Mesial to the pectoral spine, which is inserted well above the base level of the girdle, the ventral lamina carries a prominent first intermediate spine (*isp1*). All of the spines are ornamented with characteristically-noded, climatiid ribs, and are basally open. The pinnal ornament shows pronounced regional variation. On the ascending lamina it comprises low, broad tubercles (Text-fig. 29A, A′, Pl. 17, fig. 3), and this ornamentation is carried back on to the anterior part of the base of the scapula by modified body scales which are closely applied to its surface. It is impossible to draw a firm boundary between the ascending lamina and this field of scales. The whole region lay in the postbranchial wall and in ornamentation recalls the ascending lamina of *Erriwacanthus manbrookensis*. On the ventral lamina the ornamentation comprises high, ribbed tubercles, similar to those found in *Erriwacanthus falcatus* (Ørvig 1967, Pl. 1, fig. 1). A comparable ornamentation is produced on the posterolateral face of the base of the scapula by a field of closely applied high-crowned, body scales (Text-fig. 29A, A″, C). The visceral surfaces of the pinnal laminae are overlain by the scapulocoracoid, and cannot be observed.



Text-fig. 29. *Sabrinacanthus* gen. nov. *arcuatus* (Agassiz). Lower Old Red Sandstone. A, B, C, restorations of the shoulder-girdle in lateral, mesial and ventral views, with A′, A″ enlarged drawings of the dermal ornamentation. After BM P.53120 and P.53122. D, key-diagram for Pl. 17, fig. 1, showing internal structure in region of the pectoral spine. BM P.53122. Ditton Series, Nass House, Lydney, Gloucestershire, England.

The posterior of the two paired prepectoral spines is situated immediately anteroventral to the pectoral spine, and is laterally directed. Without question it is the topographic homologue of spine number 3 in *Climatius* and *Erriwacanthus*. The anterior spine is carried immediately anteroventral to the posterior, and is also laterally directed. For these reasons it is determined as paired prepectoral spine 2. The alternative determination as spine number 1 is rejected, because unlike the first spine in *Climatius* it is not ventrally directed, and it is not separated from spine number 3 by a distinct gap. It follows from the determinations of these spines and the inclusion of the first intermediate spine in the girdle, that the dermal skeleton comprises first and second middle pinnal plate and posterior pinnal plate components. There is no external sign of the division of the skeleton into its components by sutures, and no evidence of an anterior pinnal plate component.

Endoskeletal girdle. This is unusually well preserved and comprises perichondrally ossified scapular (*sc*), coracoid (*co*) and coracoid process (*pr.co*) regions (Text-fig. 29B). These regions merge smoothly with each other in the middle region, and therefore do not have sharply defined proximal boundaries. Dorsally the scapula forms a high, narrow, oval shank, which is quite distinct from the broad scapular blade of *Ptomacanthus* but is comparable with *Climatius*. Ventrally this region is anteroposteriorly expanded, and from here the mesial wall of the scapulocoracoid sweeps down over the ventral pinnal lamina in a hollow curve. The coracoid process is contained within the ventral and ascending laminae of the anterior half of the pinnal plate. The cavity of the lower region of the scapulocoracoid (originally solid cartilage) is partitioned by two stout endoskeletal laminae, which are discernible in the undissected girdle as slight ridges on the surface of the perichondral bone. The posterior lamina (*Pl.la.p*) lies in the plane of the junction between the pectoral and first intermediate spines. It is now possible to interpret the visceral ridge which runs along the anteromesial margins of the posterior pinnal plate in *Climatius reticulatus*. It may have supported the base of an exactly comparable endochondral lamina, whilst other parts of the ridge supported the mesial perichondral wall of the coracoid and coracoid process (*rdg.Pl*, Text-fig. 26B). The anterior partition in *Sabrinacanthus* (*Pl.la.m*) lies between the planes of paired prepectoral spines 2 and 3, and thus divides the regions of the scapulocoracoid associated with the first and second middle pinnal plates. There is neither evidence of a homologous lamina in *Climatius reticulatus* (paired prepectoral spine 2 is absent), nor of a partition at the posterior margin of the anterior pinnal plates. Thus in *Sabrinacanthus* there is evidence of the division of the girdle into its component pinnal regions, despite the absence of any indication of this in the dermal skeleton.

Laterally, the middle region of the scapulocoracoid extended in life into the cavity of the pectoral spine. In two specimens (P.53120a, b; P.53123a, b) the base of the resulting lateral process is partly perichondrally ossified on its posterior surface, and thus provides some information on the fin articulation area. At the base of the spine, facing posteriorly, there are horizontal dorsal and ventral muscle attachment surfaces (*dmf*, *vmf*, Text-fig. 29B). Each is in the form of a shallow trough.

Between them, in an unossified area, there must have been a short, horizontal margo radialis (*mr*). The position and small size of the muscle attachment areas, taken with the immobility of the pectoral spine, suggests that the fin muscles were smaller and less differentiated than those of *Acanthodes*.

During the negative preparation of P.53122a, b the inner face of the lateral wall of the scapulocoracoid was observed, in the region of the pectoral spine (Pl. 17, fig. 1, use Text-fig. 29D as key drawing). Both above and below the opening of the cavity of the pectoral spine (*cav.p.sp*), the perichondral bone is irregularly grooved and perforated by fine foramina (*dnvs*, *vnvs*). I interpret these features as evidence for dorsal and ventral neurovascular systems. Their relationship to the scapulocoracoid and pectoral fin is similar to that of the cutaneous nerves and vessels which penetrated the shoulder-girdle in a number of placoderms (Stensiö 1944, 1959).

There are no major foramina in the walls of the scapulocoracoid which might be compared with the coracoid foramen and subscapular fossa of *Acanthodes*. The fin of *Sabrinacanthus* must, therefore, have been innervated solely by metazonal nerves.

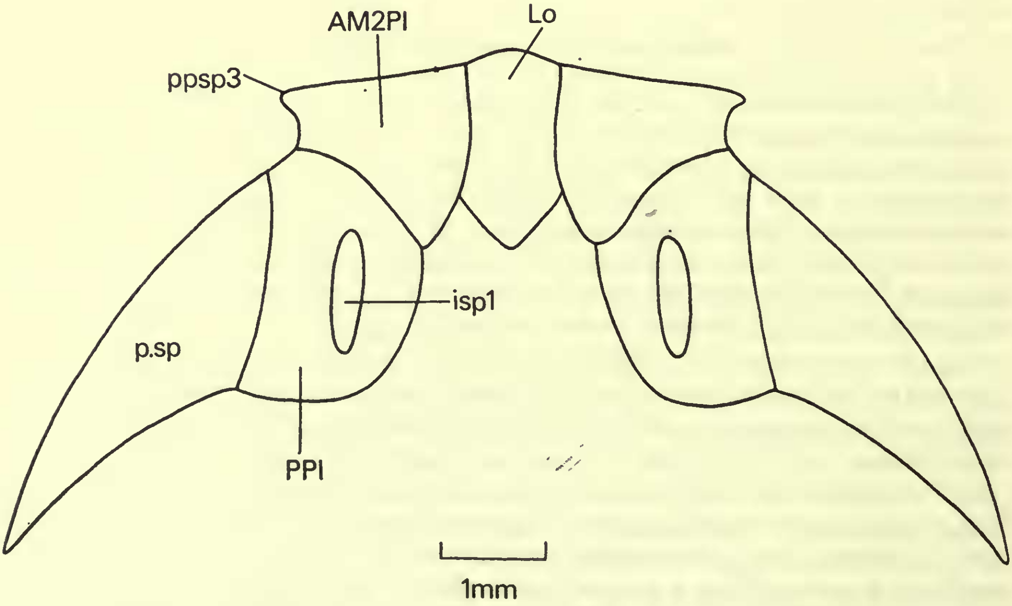
PECTORAL FIN. This structure is represented only by the curved, ribbed pectoral spine. It is seen in Pl. 17, fig. 2 (also Ørvig 1967, Text-fig. 3, Pl. 1, fig. 2), and requires no additional description. In orientation it corresponds closely with the spine of *Climatius reticulatus* (p. 166).

Brachyacanthus scutiger Egerton

This is the smallest and least well preserved of the Scottish Lower Old Red Sandstone climatiiforms, and its shoulder-girdle cannot be worked out in the same detail, or with the same degree of confidence, as in other species. I have recently classified *Brachyacanthus* with the Climatiidae (Miles 1970 : 362), although prior to this it was placed in the Euthacanthidae (Berg 1958; Miles 1966). This move is supported by the structure of the shoulder-girdle, although it was first suggested by the dermal skeleton of the head (Watson 1937, Text-fig. 5) and the apparent presence of small teeth in GSE 10408 from Duntrune Quarry, Angus.

DERMAL SKELETON. The following tentative interpretation (Text-fig. 30) is suggested by BM 35908 and P.6957, both from Farnell, Angus. The short pectoral spine (*p.sp*) is attached to a well-developed posterior pinnal plate (*PPl*; ? 'enlarged scale', Watson 1937 : 70), which bears the basally-open first intermediate spine (*isp1*). Anteromesially the posterior pinnal abuts against the ventral lamina of a further paired plate which carries a laterally-directed prepectoral spine. This plate is probably the 'anterolateral dermal bone' of Watson (1937, Text-fig. 5); mesially it is connected to a median lorical plate. The 'antero-lateral' is not easy to homologise with the plates of *Climatius reticulatus*, but because it is in contact with both the posterior pinnal and a lorical plate, it may be regarded as an anterior-middle pinnal plate (*AM2Pl*). Its spine, which is not separated from the plate by a distinct suture, may be tentatively determined as paired prepectoral spine 3 (*ppsp3*), although until the composition of the plate is known in detail it might equally well be regarded as paired prepectoral spine 2. Like the first intermediate spine, it has a distinctive ornamentation of ridges, similar to those of the pectoral spine. The median plate is too extensive to be readily accepted as the topographic homologue of the anterior lorical, and it may equal both the anterior and posterior loricals of *Climatius*. No transverse suture can be seen dividing the plate, but such is the preservation that one could well have existed. The plate is provisionally termed the lorical (*Lo*). I have not observed a median prepectoral spine, but again one might well have existed and not be discernible in the specimens at hand. The three plates just described appear to be ornamented bones not covered by scales, and they are not subdivided into scale-like areas.

Endoskeletal girdle. The scapulocoracoid is ossified as a scapula, which has been accurately figured and described by Watson (1937 : 69, Text-fig. 5). This structure is closely comparable with the scapulae of other climatiids, and it would be superfluous to redescribe it. The only new information is provided by BM P.6984 from Denoon, Angus, in which the lateral surface of the scapula is ornamented in its lower regions with fine, well-spaced tubercles. A prolonged examination suggests that this is because a group of body scales of normal size has become firmly united to the scapula.



Text-fig. 30. *Brachyacanthus scutiger* Egerton. Lower Old Red Sandstone. Plan of ventral surface of shoulder-girdle. After BM P.6957, 35908. Arbuthnott Group, Dundee Formation, Farnell, Angus, Scotland.

PECTORAL FIN. Only the spine is known. It is shown in outline in Text-fig. 30, and has been described in some detail by Watson (1937 : 69).

Ptomacanthus anglicus

It is desirable to give a brief summary of the shoulder-girdle in this species, in the light of the more primitive dermal structures described above in other climatiids.

DERMAL SKELETON. The pinnal plate(s) probably comprises a deeply-seated sheet of thin bone with ventral and ascending laminae (p. 164). Its detailed composition is not clear, but the paired prepectoral spines have a position comparable with those of *Climatius* and may be determined as numbers 1 and 3 (*ppsp1*, *ppsp3*, Text-fig. 4). The first intermediate spine may or may not have been attached to the girdle (p. 122), but it appears that the pinnal plate extends posteriorly below the coracoid region, mesial to the pectoral spine. Thus the pinnal plate is provisionally regarded as including anterior, second middle (p. 164) and posterior components (*AM2PPl*). It is covered by scales, which may represent the superficial layer of the dermal skeleton, as in *Climatius* and *Erriwacanthus manbrookensis*, but may alternatively, because of their form, represent a secondary extension of the trunk squamation over the girdle. The scales have broad, flat crowns on the ascending lamina, as in *Sabrinacanthus*. There is a median prepectoral spine (*ppsp.m*) and, therefore, probably an anterior lorical plate. There is no evidence of a posterior lorical plate.

ENDOSKELETAL GIRDLE. This is notable for the high, broad scapula (*sc*), deep coracoid (*co*) and well formed coracoid process (*pr.co*, Text-fig. 4).

Ptomacanthus sp. indet 1

I shall describe here two shoulder-girdles from the Old Red Sandstone of England which show well some of the detail of the scapulocoracoid. Both specimens closely recall *Ptomacanthus anglicus*, but they are from a different stratigraphical horizon and appear to differ in some details of form from this species. Empiric evidence suggests that individual species of fishes have a short vertical range and limited lateral distribution in the *Pteraspis crouchi* zone of the English Old Red Sandstone (White 1950 : 58, footnote). For these reasons the specimens are not given a trivial name. They seem clearly to be conspecific with each other.

MATERIAL AND LOCALITIES. BM P.17290–1, the right half of a shoulder-girdle in part and counterpart, slightly incomplete and negatively prepared, from Castle Mattock quarry, Cladock, SW. Herefordshire. BM P.23789, the right half of a shoulder-girdle seen in lateral view, from Wern Genni quarry, SW. Herefordshire.

HORIZON. Ditton Series. Castle Mattock quarry is about 73 m and Wern Genni quarry about 198 m above the main '*Psammosteus*' Limestone (White 1950 : 58, footnote); in the *Pteraspis crouchi* zone.

Description. The restorations (Text-figs 31, 32) are based mainly on P.17290–1 (Pl. 19, fig. 1) and show the salient features of the scapulocoracoid and pectoral spine. The spine (*p.sp*) is broad, gently curved and somewhat triangular in cross-section. It is ornamented with prominent ridges which become slightly beaded proximally. These ridges are, however, missing most proximally where the spine was inserted in the body wall and attached to the girdle. The cavity of the spine opens proximally on its mesial face (*cav.p.sp*), but was presumably filled with an extension of the girdle in life, as in *Sabrinacanthus*.

The scapulocoracoid is invested by a thin coat of perichondral bone. The scapular blade (*sc*) is broad and thin (see section, Text-fig. 31). It is incomplete dorsally in both specimens. The mesial face of the middle region lacks perichondral bone, adjacent to the opening of the pectoral spine cavity (*cart* (*mr*), Text-fig. 32). This region of the girdle probably included the margo radialis and muscle attachment areas, as in *Sabrinacanthus*. The coracoid region (*co*, Text-fig. 31B) merges smoothly with the more dorsal parts of the girdle. The long coracoid process (*pr.co*) is more or less triangular in section proximally (posterolaterally), with ventromesial, dorsomesial and lateral faces, but distally it tapers and becomes almost oval in section. The dorsomesial face is hollowed, except most laterally, and it may have provided a surface for the origin of hypobranchial muscles. The ventromesial face is featureless. The lateral face cannot be seen in P.17290–1, either because it was not ossified or more probably because it has not been successfully exposed by negative preparation. P.23789 has been partly prepared to show this wall, and although the specimen is not entirely satisfactory, it seems clearly to demonstrate the absence (post-mortem) of prepectoral spines. What is not clear is whether any thin dermal bone remains on the lateral and ventral surfaces of the coracoid and coracoid process.

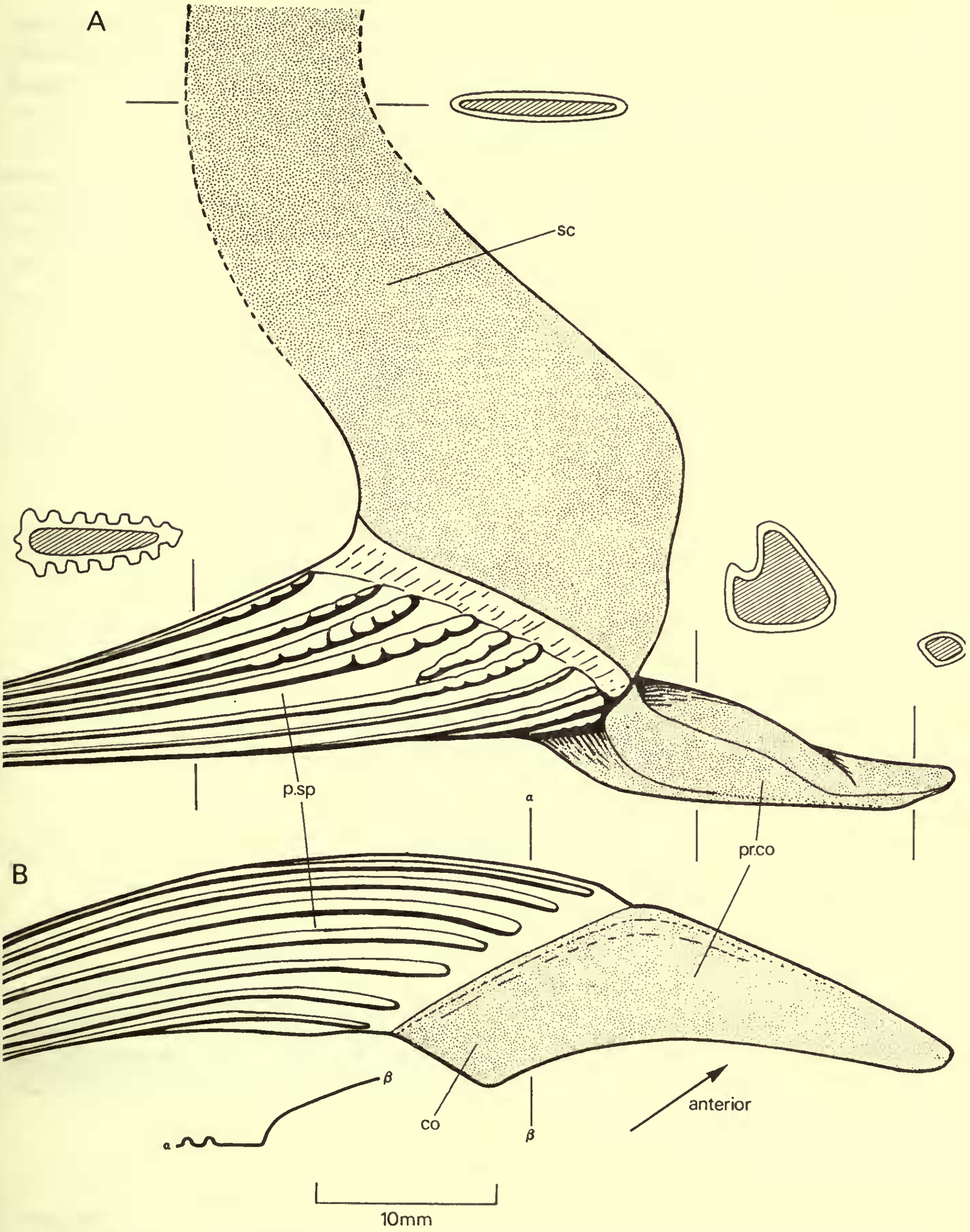
The tips of the left and right coracoid processes probably touched in the middle line, and they may have been firmly united by ligaments.

Ptomacanthus sp. indet 2

Although it adds little to our knowledge in connexion with the present paper, it is interesting to record the existence of a shoulder-girdle of *Ptomacanthus* sp. (SMNH P.6841; cast BM P.53040) from the Dittonian of Zaleszychi, Ukranian SSR, which closely resembles *Ptomacanthus* sp. indet 1. This specimen (Pl. 20, fig. 1) confirms the high tapering form of the scapular blade.

Vernicomacanthus uncinatus (Powrie)

All the remaining species of Devonian climatioids to be described are alike in the complete reduction of the ventral laminae of the pinnal plates, and therefore in the suppression of the posterior pinnal and in the separation of the pectoral and first intermediate spines from the dermal plates. The pinnal plates are represented

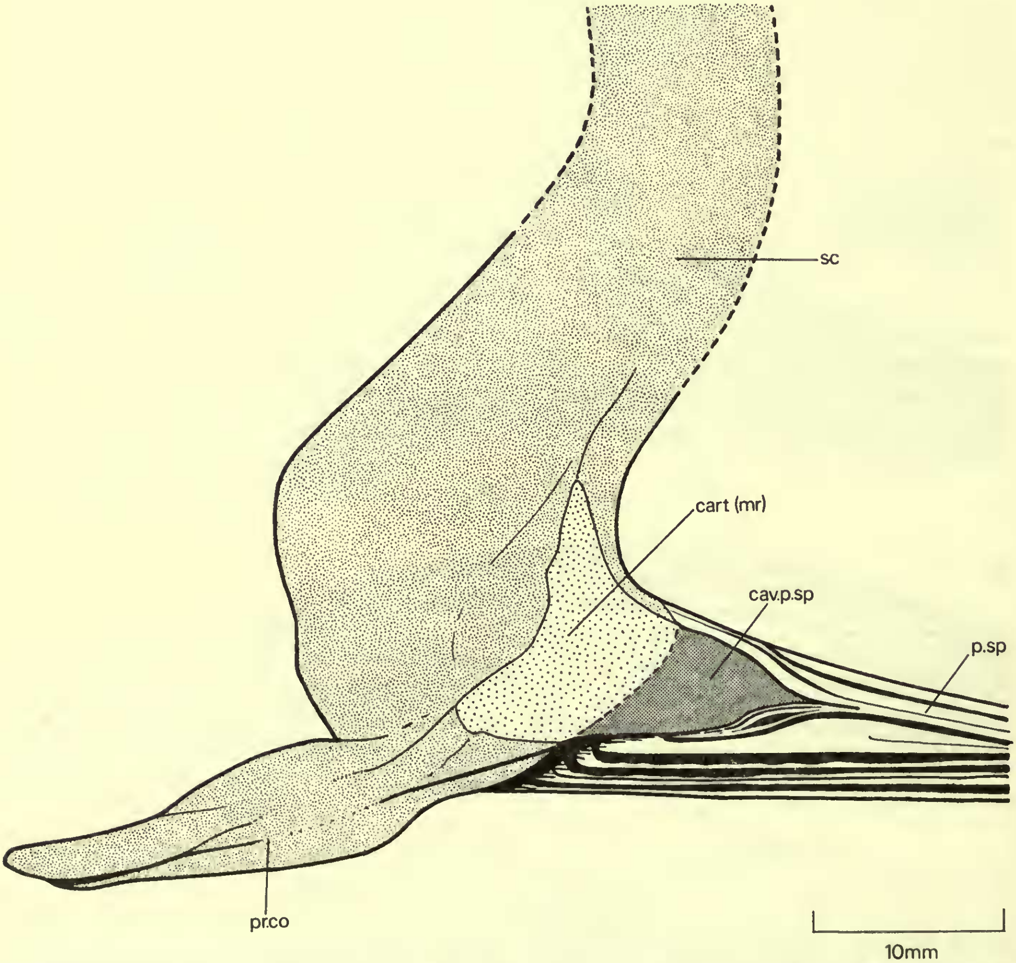


TEXT-FIG. 31. *Ptomacanthus* sp. indet. 1. Lower Old Red Sandstone. Restoration of shoulder-girdle in A, lateral and B, ventral view with sections and profile A–B as indicated. After BM P.17290–1. Ditton Series, Castle Mattock quarry, Cladock, Herefordshire, England.

solely by their ascending laminae and accompanying paired prepectoral spines. These laminae were situated in the hind wall of the branchial chamber, immediately in front of the scapulocoracoid. The posterior lorical has also been suppressed in all of these species, although the anterior lorical is retained in some and may have both ventral and ascending laminae.

The above statements are based on the assumption that *Climatius reticulatus* is a more primitive species than those which follow. This assumption is explained below (p. 195).

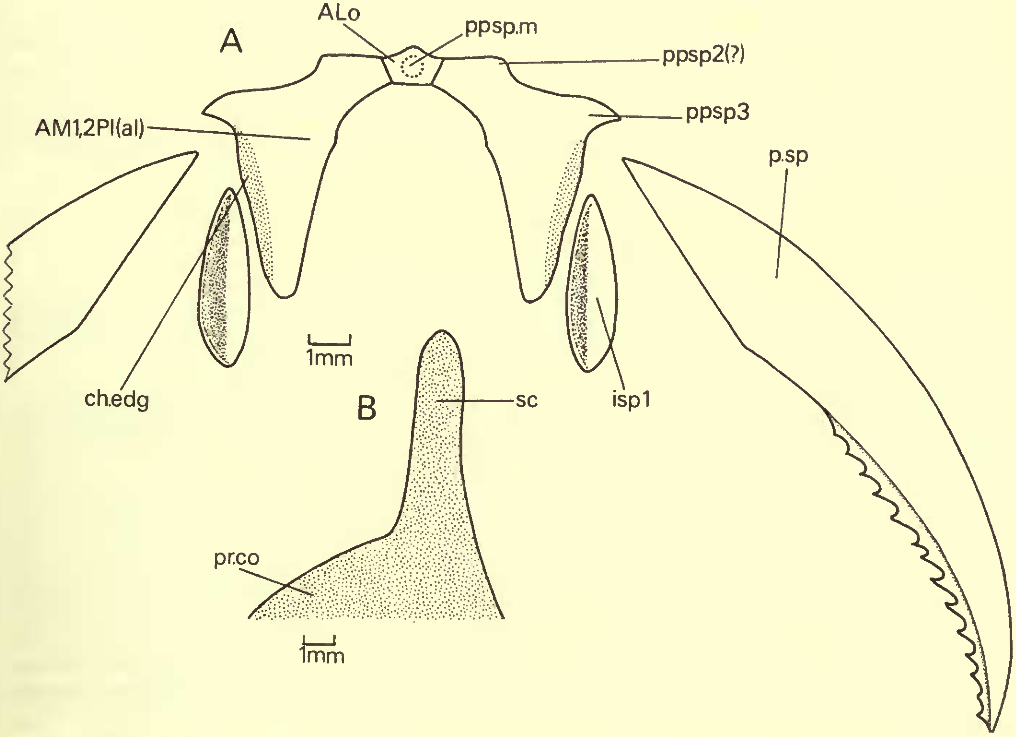
Climatius uncinatus Powrie has been referred to the new genus *Vernicomacanthus* on p. 140.



Text-fig. 32. *Ptomacanthus* sp. indet 1. Lower Old Red Sandstone. Restoration of shoulder-girdle in mesial view. After BM P.17290–1. Ditton Series, Castle Mattock quarry, Cladock, Herefordshire, England.

DERMAL SKELETON. There is an anterior lorical (*ALo*) and a compound ascending lamina which represents the anterior and one or two middle pinnal plates (*AMPl*, Text-fig. 33, Pl. 7). The anterior lorical is arched and ends in a distinct dorsal angle, but the ventral and ascending laminae do not quite form a hemicylinder. Ventrally the plate carries a short median prepectoral spine (*ppsp.m*) which has a large central cavity.

The ascending pinnal lamina sutures with the ascending lamina of the anterior lorical plate. Laterally the pinnal lamina bears a short, basally open spine, which may be regarded as paired prepectoral spine 3 (*ppsp3*) by comparison with other genera. Further forwards the lamina is expanded into a lateral elbow, three mm or so to the side of the anterior lorical plate. I provisionally accept this as the site of a small prepectoral spine, which is too badly preserved to be observed clearly. By comparison with *V. waynensis* (p. 180, Text-figs. 14, 15A) it is determined as paired prepectoral spine 2. As the ascending lamina sutures with the anterior lorical plate, it is assumed to include an anterior pinnal plate component. Thus the



TEXT-FIG. 33. *Vernicomacanthus* gen. nov. *uncinatus* (Powrie). Lower Old Red Sandstone. A, plan of shoulder-girdle in dorsal view, position of median prepectoral spine on ventral surface shown with dotted line. B, lateral view of scapulocoracoid. After RSM Kinnaird collection 82, 1891.92.210, BM P.1342a. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

ascending lamina comprises components of the anterior, and first and second middle pinnal plates (*AM1,2Pl*). The posterior margin of the pinnal lamina is bevelled (*ch.edg*), where the plate emerges laterally from the postbranchial wall.

The lorical and pinnal dermal plates show no sign of subdivision into scale-like areas and are ornamented with irregularly arranged, flat-topped tubercles which are transformed into three or four ill-defined ridges on paired prepectoral spine 3. The median prepectoral spine bears a few small tubercles. The pectoral spines have the normal climatioid ribbed ornamentation, but unlike other Scottish Lower Old Red Sandstone species, the ridges are obliquely placed as in *Gyracanthus incurvus* Traquair from the Lower Devonian of Canada (Woodward 1892a, Pl. 1, fig. 4). There is also a series of prominent denticles on the trailing edge of the spine. The first intermediate spine is situated mesially to the base of the pectoral spine. These two spines and the anterior lorical plate are separated from each other by regular rows of body scales (Pl. 7).

ENDOSKELETAL GIRDLE. The scapula is perichondrally ossified, with a coracoid process, and it has a similar relationship to the pectoral spine and dermal girdle as in other climatioids. The figure (Text-fig. 33B) requires no further comment.

PECTORAL FIN. The endoskeleton and dermotrichia of the fin are unknown, but minute scales from the ventral surface of the web are preserved in BM P.6960 and RSM 1891.92.210. These scales appear to lie in rows across the web rather than in proximo-distal rows, but this may be an artifact of preservation. The shape and size of the web are unknown, although clearly it was well developed.

Vernicomacanthus waynensis

This species has been described in the first part of this paper (p. 140). The composition of the dermal shoulder-girdle may be summarised here in the light of the results gained so far.

There are two paired prepectoral spines carried by an undivided ascending pinnal lamina. The posterior spine (*ppsp3*, Text-figs. 14, 15A) is situated immediately anteroventral to the pectoral spine, and by comparison with forms such as *Erriwacanthus*, *Climatius* and *Sabrinacanthus*, it can be confidently determined as paired prepectoral spine 3. The anterior spine (*ppsp2*) lies immediately in front of spine number 3. I have determined it as paired prepectoral spine 2, as indicated above in the description of *V. uncinatus*, because of its position and because it is ventrolaterally directed. Paired prepectoral spine 1 is more ventrally directed and more ventromesially situated than this in *Erriwacanthus falcatus* and *Climatius reticulatus*, and I have, therefore, rejected paired prepectoral spine 1 as an alternative determination.

The anterior lorical is reduced to a large tessera without an ascending lamina, and there is no median prepectoral spine (*ALo*, Text-fig. 14). The anterior lorical has no contact with the ascending pinnal lamina. Ventrally the various spines and the anterior lorical are separated from each other by an irregular field of large scales.

The separation of the anterior lorical plate and ascending pinnal lamina raises the question of the composition of this last structure, specifically whether it includes an anterior pinnal plate component. There is no means of answering this question, but provisionally I shall assume that this component is present, as in *V. uncinatus*. The ascending lamina (*AM1,2Pl*) is then believed to include anterior, and first and second middle pinnal components, as in *V. uncinatus*. *V. waynensis* is more advanced than *V. uncinatus* in the reduction of the anterior lorical and in the separation of this plate from the pinnal lamina; it is possibly more primitive in the greater size of paired prepectoral spine 2.

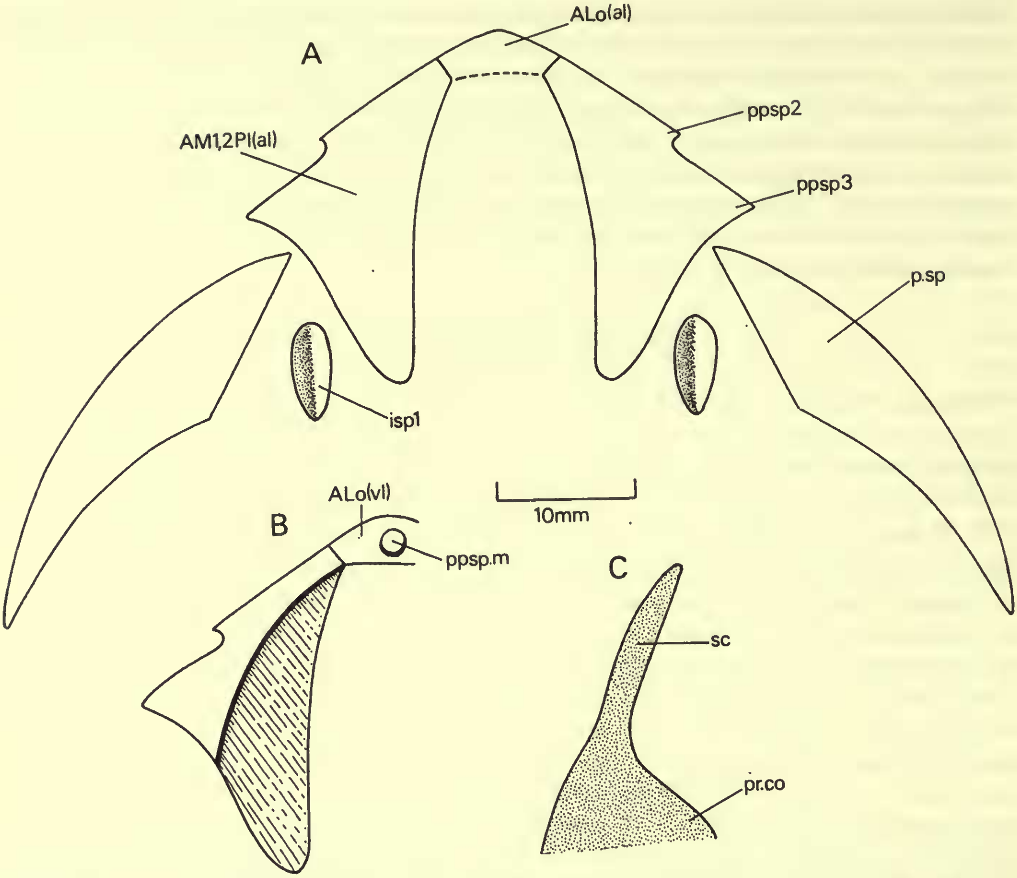
Parexus falcatus Powrie

It is convenient to describe this species before the type, *Parexus recurvus* Agassiz, because two specimens show the dermal plates of the shoulder-girdle flattened but in their natural relationship to each other. These specimens are from the Lower Old Red Sandstone of Turin Hill, Scotland, and bear the numbers RSM 1891.92.207 (Pl. 16, fig. 1) and BM P.130 (in counterpart) (Woodward 1891, Text-fig. 4; Dean 1907, Text-fig. 21). Both specimens show the lateral plates in visceral view.

DERMAL SKELETON. The ornamented dermal plates (Text-fig. 34) show no sign of subdivision into scale-like areas. They comprise the median anterior lorical (*ALo*), and a paired ascending pinnal lamina (*AMPl*, 'clavicle', Woodward 1891). The anterior lorical has a hemicylindrical section with ventral and ascending laminae which merge smoothly with each other. The ventral lamina bears a short, basally-open, median prepectoral spine (*ppsp.m*). The ascending pinnal lamina gives rise to two short, laterally-directed spines with basally-open cavities. The posterior of these spines is paired prepectoral spine 3 (*ppsp3*). The anterior may be determined as paired prepectoral spine 2 (*ppsp2*), with exactly the same arguments I have used in the case of *Vernicomacanthus waynensis*. The pinnal lamina thus comprises anterior, and first and second middle pinnal plate components (*AM1,2Pl*). As in *Vernicomacanthus* the pectoral spine (*p.sp*) and the first intermediate spine (*isp1*) stand free of the dermal shoulder-girdle. In both genera these spines retain the same spatial relationships to the surviving plates that they have in species such as *Climatius reticulatus*. Scale fields comprising slightly enlarged body scales separate the lorical plate and detached spines on the ventral surface. The scales tend to form antero-posterior rows between the paired prepectoral spines, but more posteriorly they merge with the normal body scaling.

ENDOSKELETAL GIRDLE. The preserved endoskeleton is the perichondrally ossified scapula (*sc*), which has a high cylindrical shank and a broad ventral plate which is attached to the upper edge of the pectoral spine.

PECTORAL FIN. The endoskeleton and dermotrichia are unknown, but both specimens show the fin web in the form of numerous small scales. Unfortunately these are poorly preserved, but they show that the web extended beyond the pectoral spine for a distance at least equal to half the length of the spine.



TEXT-FIG. 34. *Parexus falcatus* Powrie. Lower Old Red Sandstone. A, plan of shoulder-girdle in dorsal view. B, plan in ventral view, with right plates omitted; C, lateral view of scapulocoracoid. After RSM 1891.92.207, 1887.35.4, BM P.130. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

Parexus recurvus Agassiz

Since Powrie (1864, 1870), there has been a tendency to refer to this species in the incorrect form *Parexus incurvus* (Woodward 1891; Watson 1937; Westoll 1945; Ørvig 1967). The correct form will, however, be found in Traquair (1894a, b) and Waterston (1954). *Parexus recurvus* occurs in the Lower Old Red Sandstone of Turin Hill, and it is said to differ from *P. falcatus* in its smaller size, relatively smaller head and relatively longer, straighter first dorsal fin-spine. Whether this species separation is justified is perhaps open to question, as some of these differences can be accounted for by the normal processes of growth. With respect to the shoulder-girdle there appear to be no important differences of structure. The following notes, therefore, are given to supplement the account of *P. falcatus*. They are based on RSM 1956.14.14, 1887.35.3A, 1891.92.190 and 1891.92.188.

Dermal skeleton. The ascending pinnal lamina has been mistaken for a ventral plate by Watson and Ørvig ('antero-lateral dermal bone', Watson 1937; 'ventrolateral plate', Ørvig 1967). It is ornamented with irregular rows of flat, leaf-like tubercles, which become smaller and more regularly arranged on the paired prepectoral spines (Pl. 19, fig. 2; Ørvig 1967, Pl. 1, fig. 31). The posterolateral margin of this lamina is bevelled almost to the tip of paired prepectoral spine 3, as in *Vernicomacanthus uncinatus* (p. 180). The anterior lorical plate is also ornamented with flat tubercles, but these are arranged in tightly-packed rows which run mostly in the antero-posterior direction, although they converge on the spine. Both the median and the paired prepectoral spines are basally open.

Endoskeletal girdle. The scapular ossification is exactly comparable with that of *Parexus falcatus*. RSM 1891.92.188 and 1891.92.190 are of particular interest because they have enlarged body scales closely applied to the lateral surface of the shoulder-girdle (Text-fig. 35). These scales are about twice as big as the adjacent flank scales and are arranged in irregular antero-posterior rows. A similar patch of scales is less well seen in *P. falcatus* (BM P.130; Dean 1907 : 217, Text-fig. 27).

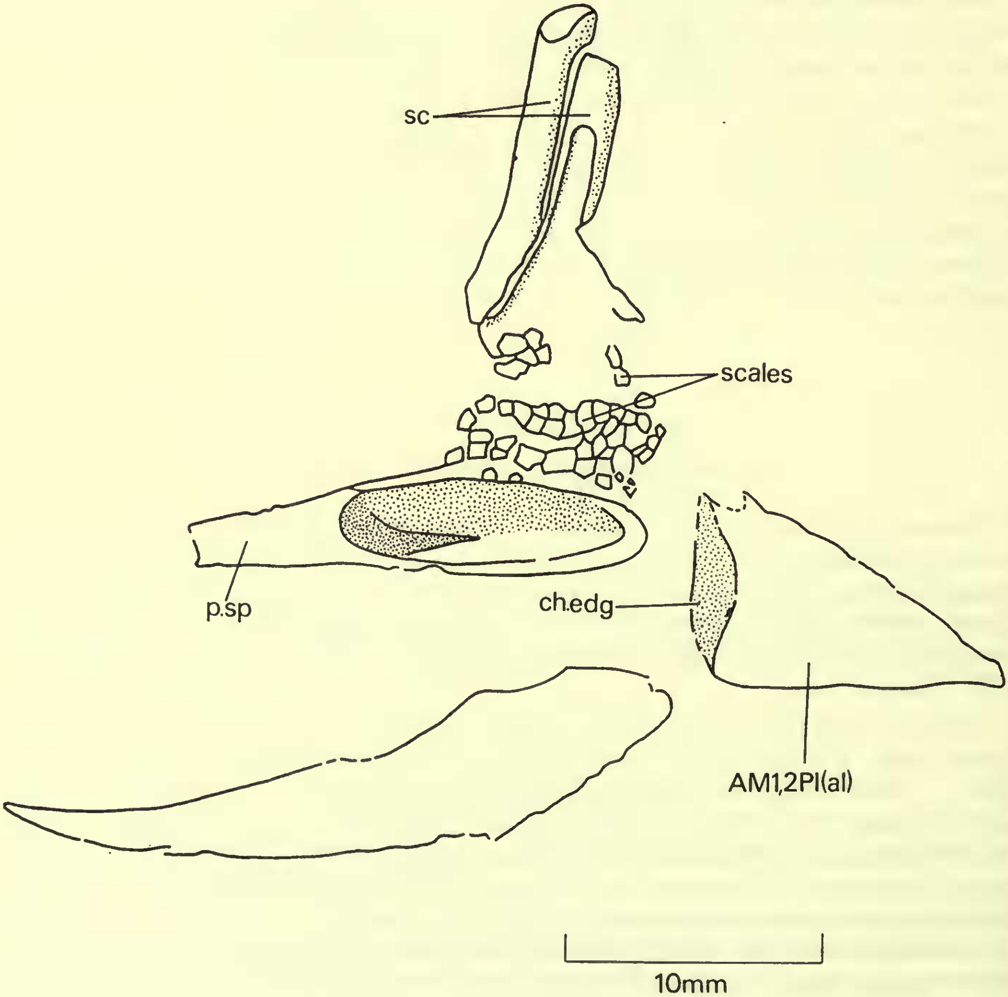
Family **EUTHACANTHIDAE**

Euthacanthus macnicoli Powrie

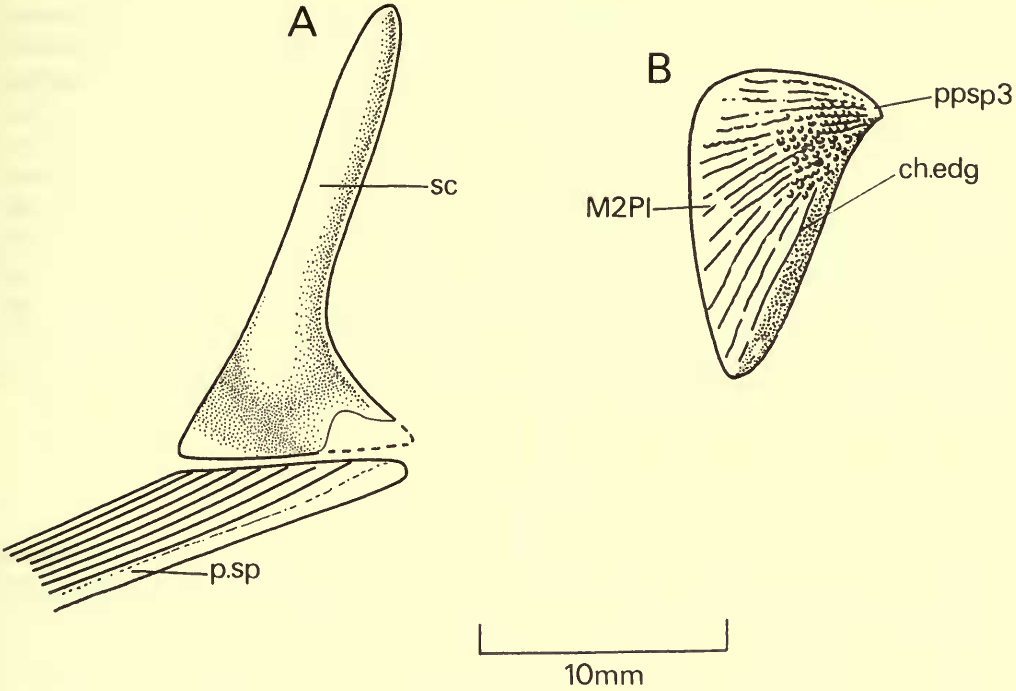
Powrie (1870) recognised five species of *Euthacanthus* in the Lower Old Red Sandstone of Scotland, but only one of these, *Eu. macnicoli*, is well known, and the classification of the genus is in an unsatisfactory state. The following account is based on the type specimen of *Eu. macnicoli* (RSM 1891.92.231 – BM P.1337, counterparts) and two others referred to this species, RSM 1887.35 and GSM 88923 (Pl. 18, fig. 2).

Dermal skeleton. The dermal girdle consists of a single pair of ornamented plates which are each produced laterally into a flattened, horizontal spine (Text-fig. 36B). There is no suture between the plate and the spine. Watson (1937, Text-fig. 4) interpreted each plate as a ventral element ('antero-lateral pectoral dermal bone'), but the size and relationships of the plate suggest that it should be termed the ascending lamina of the second middle pinnal plate (*M2Pl*, Text-fig. 36B), and thus the spine is paired prepectoral spine 3 (*ppsp3*). The posterolateral edge of the plate is bevelled (*ch.edg*), like the corresponding margin in *Parexus* and *Vernicomacanthus*. The ornamentation comprises large leaf-like tubercles which run in rows and tend to fuse into ridges (Pl. 18, fig. 2). The ridges become finer on paired prepectoral spine 3 and converge on its tip. The visceral surface of the lamina is unknown. No other plates are found in the girdle, and there is no evidence of other prepectoral spines, or of a pair of intermediate spines, between the bases of the ribbed pectoral spines. Watson's (1937, Text-fig. 4) restoration shows the 'first' intermediate spine (see p. 197 *infra*) more posteriorly situated, between the tips of the pectoral spines.

ENDOSKELETAL GIRDLE. The perichondral scapular ossification (*sc*) has a similar shape and extent to that of other Lower Devonian species (Text-fig. 36A). The lateral surface of the scapulocoracoid is coated with enlarged body scales which run in irregular rows. They are well seen in the type specimen (Watson 1937, Pl. 7, fig. 2), and reach about twice the size of the adjacent flank scales. They do not fuse to form lateral shoulder-girdle plates.



TEXT-FIG. 35. *Parexus recurvus* Agassiz. Lower Old Red Sandstone. Sketch of shoulder-girdle, RSM 1891.92.190. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.



TEXT-FIG. 36. *Euthacanthus macnicoli* Powrie. Lower Old Red Sandstone. A, scapulocoracoid and proximal region of pectoral spine in lateral view. B, right ascending pinnal lamina with paired prepectoral spine 3. After GSM 88923 and RSM 1887.35. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

PECTORAL FIN. Again the endoskeleton of the fin is unknown, as are the dermotrichia. Watson (1937 : 65) records that the fin web 'is often visible as an area covered with very small square scales'. This condition is well seen (Pl. 15, fig. 1) in a specimen of unknown history in the RSM, which I have tentatively determined as *Euthacanthus* sp. Here the scales run in long, lepidotrichia-like rows, which converge on the base of the fin. They show that the web was extensive and the base relatively narrow.

Family **GYRACANTHIDAE**

The relations of gyracanthids were quite unknown until Woodward (1906) described *Gyracanthides murrayi* from the Carboniferous of Australia and showed that it was an acanthodian. For *Gyracanthus* spp. (type *G. formosus* Agassiz) and *Gy. murrayi* he erected the family Gyracanthidae, which was defined as follows: '. . . round-bodied and depressed Acanthodians, with the pectoral fins very large and the pelvic fins advanced far forwards. Dorsal and anal fins much reduced and sometimes apparently without spines'. When I published my classification of acanthodians (Miles 1966), I felt that a close relationship between *Gyracanthides* and *Gyracanthus* had not been demonstrated, and that profitable discussions of the structure and relationships of Carboniferous climatiiforms could only be based on the Australian genus. From this I was led into the error of listing *Gyracanthides* as the type genus of the family Gyracanthidae Woodward.[4] Subsequently I erected the family Gyracanthididae for this genus (Miles 1971). Further study of gyracanthids, however, has convinced me that the family Gyracanthidae should be retained in its original sense (type *Gyracanthus*), and that it is proper to refer both *Gyracanthides* and *Oracanthus* to this family. Woodward's definition may be amended to include: 'shoulder-girdle with paired prepectoral spine 3'. Because of the structure of the shoulder-girdle, the Gyracanthidae may be placed in the Climatioidei.

Gyracanthus formosus Agassiz

It is only necessary to consider the type species in this paper; it is the best known species. Traquair (1884) has discussed the paired fin-spines in some detail, and concluded incidentally that dorsal fin-spines were not present. The 'carpal bones' of Hancock & Atthey (1868) are of particular interest. Traquair (1884 : 44) correctly concluded that they were 'dermal appendages . . . situated in the neighbourhood of the pectoral fin', and pointed out that they were hollow and often badly crushed. The variation in form noticed by some authors is due partly to this crushing and partly to incomplete preservation.

One specimen (BM 45864, Pl. 21) makes the structure of the 'carpal' element clear. It is from the 'Coal Measures of Newcastle upon Tyne', and although the locality is not recorded it is probably from the Low Main Seam, Newsham. The specimen comprises a hollow, curved spine, i.e. the 'triangular bone' which is normally preserved, and a dermal plate (Text-fig. 37). No visible suture separates the spine from the plate, and the free surfaces of both are extensively ornamented with flat, fine anastomosing ridges. There are no sure means of orientating the specimen, but it appears most probable that the greater part of the plate formed a ventral lamina, and that it includes a low lateral lamina behind the spine. If this is correct, I estimate that the spine is directed posterolaterally and very slightly ventrally, with its long axis set at about 10° from the horizontal. In transverse section it is oval, and is tilted at about 45°, with its leading edge higher than its trailing edge. The wide cavity of the spine is open (*cav.sp*) and is bounded posteriorly on the visceral surface of the dermal plate by a high, stout endoskeletal ridge (*Pl.la.p*). It is most reasonable to interpret the spine as paired prepectoral spine 3, as this is the only spine invariably present in climatioids. The endoskeletal ridge may thus be compared with the posterior endoskeletal lamina in *Sabrinacanthus*. From this

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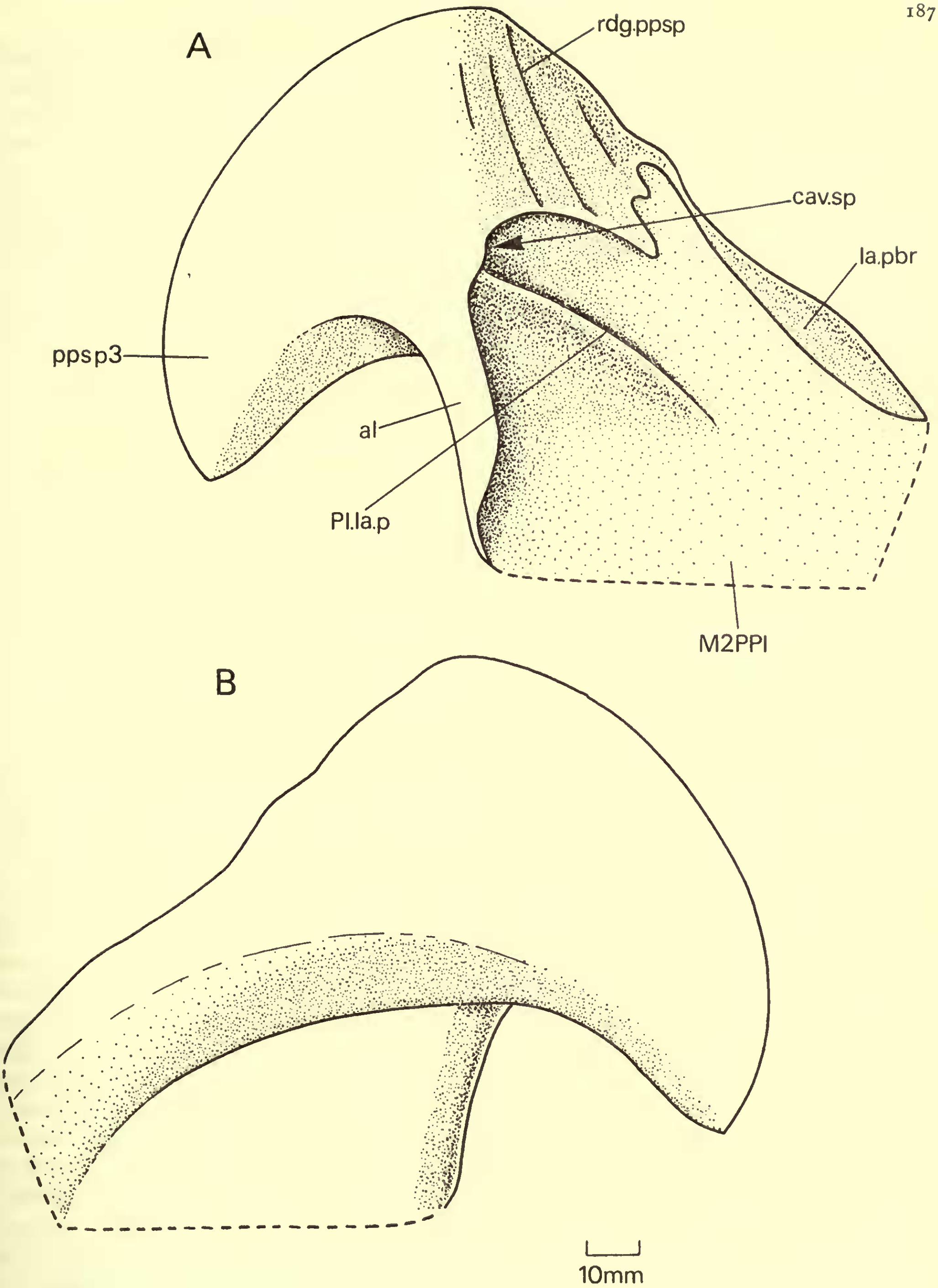
[4] I am indebted to Drs C. Patterson and D. Baird for independently bringing this mistake to my attention, shortly after the publication of my paper.



Text-fig. 37. *Gyracanthus formosus* Agassiz. Upper Carboniferous. Restoration of dermal plate and paired prepectoral spine 3 in A, dorsal and B, ventral view. After BM 45864. Low Main Seam, Newsham, Northumberland, England.

it follows that the dermal plate comprises the second middle pinnal and a much reduced posterior pinnal plate, despite its lack of contact with the pectoral spine. The anteromesial and lateral margins of the plate are raised, and form low postbranchial (*la.pbr*) and ascending (*al*) laminae respectively. Both laminae merge smoothly with the prepectoral spine, and the first bears a series of broad, low ridges separated by narrow grooves (*rdg.ppsp*). The presence of an ascending lamina posterior to the spine is unusual in comparison with Devonian climatioids.

There can be no doubt that the spine and plate just described were carried immediately in front of the pectoral spine and main parts of the scapulocoracoid. Unfortunately this last structure and the pectoral fin are unknown. There is no evidence of additional prepectoral or intermediate spines.

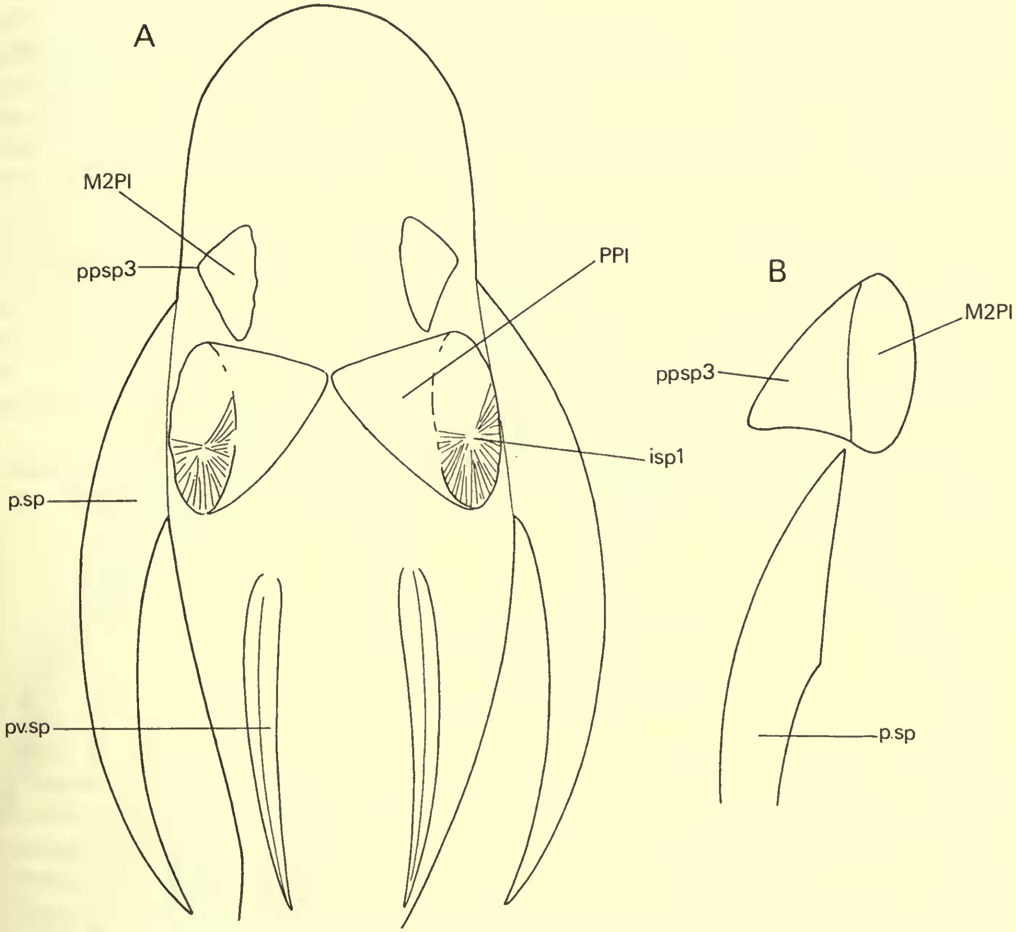
Gyracanthides murrayi Woodward

Woodward summarised his conception of this species in a single restored drawing (1906, Text-fig. 1). If we assume that this figure is correct, *Gyracanthides* exhibits long, curved pectoral spines (*p.sp*, Text-fig. 38A), between which lie triangular posterior pinnal plates (*PPl*; 'basal plate') which carry the first intermediate spines (*isp1*; 'posterior free pectoral spine'). Immediately in front of these structures is a separately developed paired element which might be interpreted as the second middle pinnal plate (*M2Pl*) plus paired prepectoral spine 3 (*ppsp3*; 'anterior free pectoral spine'). There are no other intermediate spines and the pelvics (*pv.sp*) lie relatively far forwards.

In some respects this restoration is strange, and the shoulder region bears little relationship to that of *Gyracanthus*. The presence of a free-lying posterior pinnal plate is particularly odd, as this is a characteristic of diplacanthoids (p. 201; Text-fig. 39A), and it suggests that *Gyracanthides* is incorrectly referred to the climatioids. However, there are grounds for believing that Woodward's restoration is incorrect.

Hills (1958 : 91) has stated that the 'anterior free pectoral spines' in the restoration are based on the tooth-plates of '*Ctenodus*' *breviceps*. This comment presumably applies to the details in Woodward's figure, and it is also likely that some detached elements have been wrongly determined, but there can be no doubt that the hollow structures termed 'anterior free pectoral spines' in the articulated specimens really belong to *Gyracanthides*. A more important point is that none of the articulated specimens shows a full set of anterior and posterior 'free pectoral spines', and that the spines are always somewhat displaced. Thus the type specimen (Woodward 1906, Pl. 1, fig. 1) shows one 'anterior free spine' and the 'oval plate closing base of posterior free pectoral spine'; another specimen (Pl. 1, fig. 7) shows only one 'free spine', termed the anterior, which is mesial to the proximal end of the pectoral spine; and yet another specimen (Pl. 2, fig. 1) shows one 'posterior free pectoral spine', situated mesial and slightly posterior to the pectoral spine. There is no direct evidence, therefore, that *Gyracanthides* had both anterior and posterior 'free pectoral spines', and Woodward's (1906 : 2, 6, 7) restoration seems to have been based on comparisons with Scottish Devonian species, then imperfectly understood.

Woodward compared the 'posterior free pectoral spines' with the triangular spines (paired prepectoral spine 3; *ppsp3*) of *Gyracanthus*. This is evidently correct, and the 'basal plate' may thus be said to include the second middle pinnal plate (*M2Pl*). Both structures must, however, have been more anteriorly situated than in the original restoration, in a prepectoral position. The 'anterior free pectoral spines' appear to be based on a misinterpretation of the same structures, and have in fact no real existence. This is supported by the type specimen in which the single 'anterior pectoral spine' is of similar size to the 'posterior pectoral spine', although according to the written description (Woodward 1906 : 7, 8) the anterior spine should be much smaller than the posterior.



TEXT-FIG. 38. *Gyracanthides murrayi* Woodward. Lower Carboniferous. A, Sketch restorations to show shoulder-girdle in ventral view, according to Woodward 1906, Text-fig. 1. B, new interpretation of dermal plate and spines of right side.

A tentative new plan of the shoulder region is given in Text-fig. 38B. This allows a direct comparison to be made with *Gyracanthus*, to which *Gyracanthides* may be closely related. The scapulocoracoid and pectoral fins are unknown.

Oracanthus milleri Agassiz

In a recent review of *Oracanthus*, Patterson (1965 : 151–152) has concluded that the genus may contain paired spines of acanthodians, and he has provided histological evidence in support of this view. The same conclusion is implicit in Woodward's (1906 : 8, 9) comparisons between the triangular ('posterior free pectoral') spines of *Gyracanthus*, *Gyracanthides* and *Oracanthus*. This conclusion suggests that the long spines of *O. milleri* are pectoral fin-spines (e.g. Davis 1883, Pl. 64, fig. 2; also *O. postulosus*, Pl. 65, fig. 1), and the short triangular spines (Davis 1883, Pl. 63, figs 1–3) are prepectoral spines. The latter were presumably carried in front of the pectoral spines, as in *Gyracanthus* and *Gyracanthides*, and are paired prepectoral spines (no. 3). There is, however, no evidence of a pinnal plate, and the whole pinnal series may have been entirely reduced. Davis's three specimens of the prepectoral spine are preserved in the British Museum (Nat. Hist.) (P.2873, P.2874, P.2875). They are hollow, ornamental structures that have been accurately figured, making it possible to discount the misleading written description (Davis 1883 : 530). One point of interest is the bevelled margin, which invites comparison with the posterolateral margin of the ascending pinnal lamina-paired prepectoral spine 3 complex of *Euthacanthus* (see also *Parexus*, *Vernicomacanthus*). The nature of the other dermal bones which have been ascribed to *Oracanthus* (Davis 1883; Patterson 1965) remains unknown.

There now seems to be sufficient evidence to refer *Oracanthus* to the Gyracanthidae, although its close affinities remain undisclosed for the want of better material.

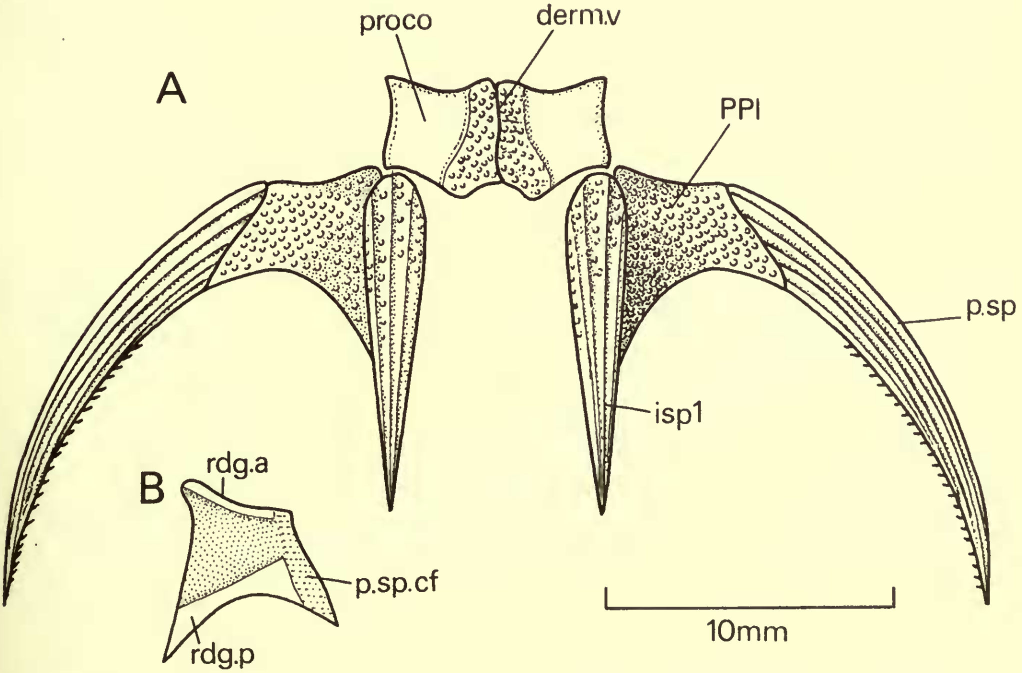
Suborder DIPLACANTHOIDEI

Family **DIPLACANTHIDAE**

Diplacanthus striatus Agassiz

Gardiner (1966 : 50) believes that the correct name for this species is *Diplacanthus crassissimus* Duff, but for reasons already given (Miles 1966 : 166, footnote 2) I retain the widely used name *D. striatus*. It is the type and best known species of *Diplacanthus*, and the only one which it is necessary to consider here. Other species appear to be almost identical in the structure of the shoulder-girdle. Woodward (1891, Text-fig. 3) and Watson (1937 : 94, Text-figs 15, 16) have described the girdle (also Traquair 1894a), but their accounts do not always agree, and some points remain to be added. The following account is based on BM 36582, P.1357a, P.1366, P.1364–4311 (counterparts) and RSM 1891.92.334 from the Middle Old Red Sandstone of Tynet Burn, Banffshire, Scotland, and casts of HU MB26 (Miles 1966, Text-fig. 10) which is believed to be from the same locality.

Dermal skeleton. If a comparison is made with climatioids, the dermal skeleton (Text-fig. 39) is represented solely by the posterior pinnal plate (*PPl*; 'basal cartilage', Woodward 1891; 'dermal plate', Watson 1937). Certain other dermal structures are considered below together with the scapulocoracoid. The posterior pinnal is arched so that the pectoral spine (*p.sp*) is carried above the base level, and the anterior margin turns up to contact the postbranchial lamina of the scapulocoracoid. Laterally the plate overlaps a narrow area at the base of the pectoral spine (Watson 1937 : 94; Miles 1966, Text-fig. 10), so that the two structures normally remain firmly united. Mesially the plate abuts against the large first intermediate spine (*isp1*; 'median spine', Woodward 1981; 'admedian pectoral spine', Watson 1937; 'ventral spine from shoulder girdle', Miles 1966). There is no evidence that these elements overlapped each other. Watson (1937 : 94) suggests that the dermal plate spreads mesially around the base of the first intermediate spine, but I have not been able to confirm this with the Tynet specimens, and do not show this condition in my restoration. The outer surface is ornamented with numerous fine, irregularly arranged

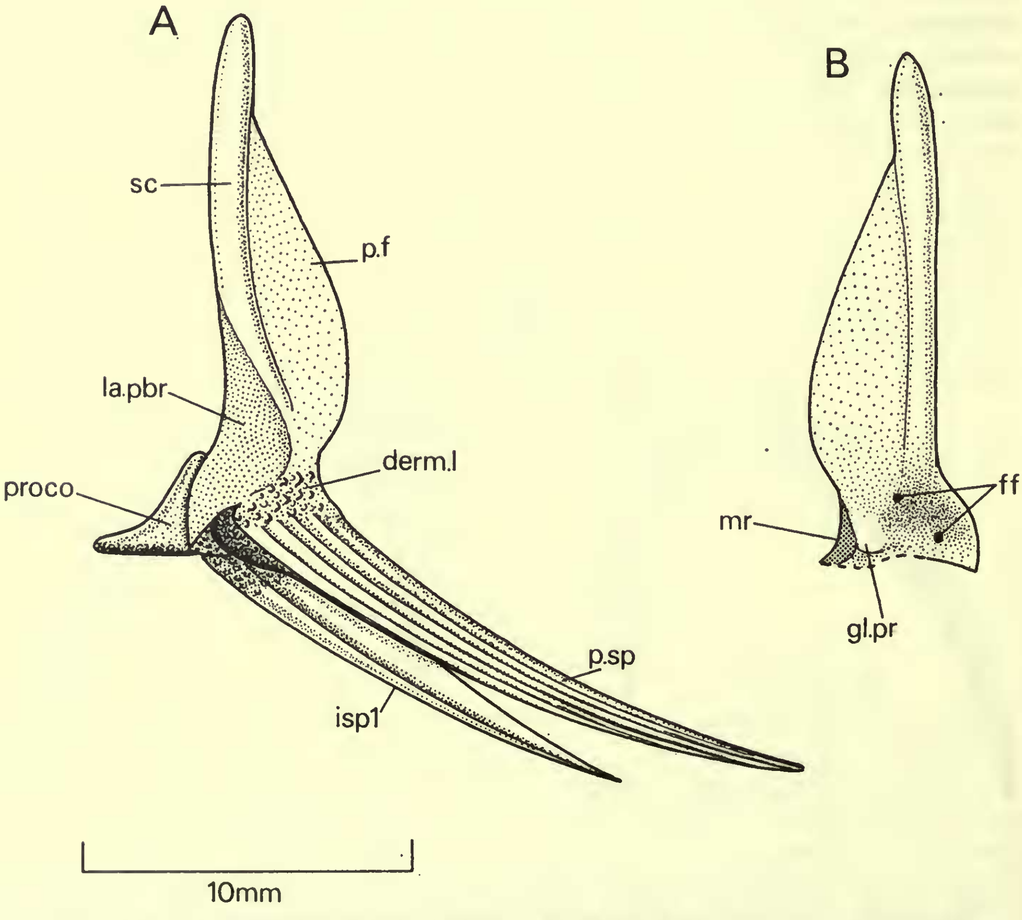


Text-fig. 39. *Diplacanthus striatus* Agassiz. Middle Old Red Sandstone. A, restoration of shoulder-girdle in ventral view; B, dorsal view of posterior pinnal plate. After BM 36582, P.1357a, P.1366, P.1364–4311 (counterparts). Tynet Burn, Banffshire, Scotland.

tubercles. The visceral surface has a smooth area laterally (*p.sp.cf*, Text-fig. 39B) for the overlap surface of the pectoral spine, and anterior and posterior ridges (*rdg.a*, *rdg.p*) which delimit a central area for the base of the unossified coracoid. These ridges are together homologous with the posterior pinnal ridge of *Climatius*, and the anterior probably received the base of a posterior endochondral lamina (cf. *Sabrinacanthus*).

The pectoral and first intermediate spines are already well known, and can be seen in the illustrations. They require no further comment.

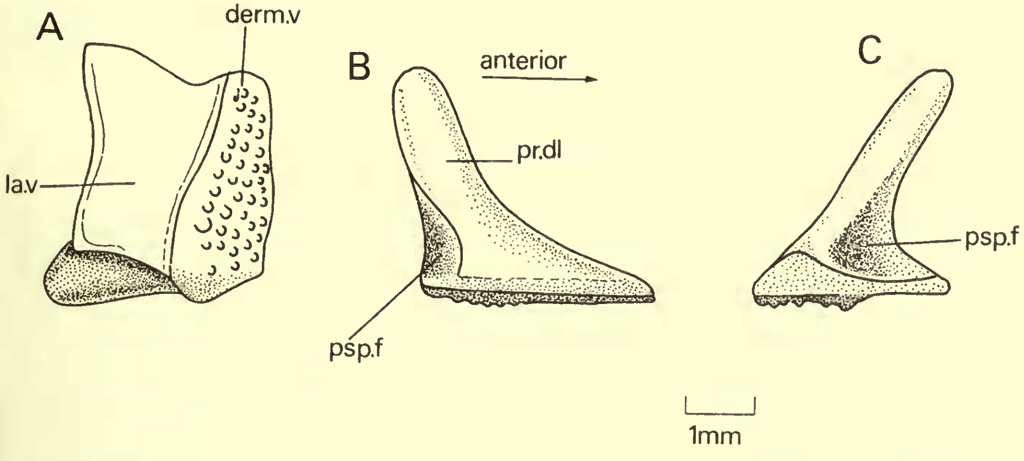
ENDOSKELETAL GIRDLE. The endoskeleton (Text-fig. 40) consists of the perichondrally ossified scapular blade (*sc*) and a separate procoracoid (*proco*). The scapula ('clavicle', Woodward 1891) comprises a vertically standing shank, with a



TEXT-FIG. 40. *Diplacanthus striatus* Agassiz. Middle Old Red Sandstone. A, restoration of shoulder-girdle in lateral view; B, scapula in mesial view. Mainly after RSM 1891.92. 334, and Watson 1937, Text-fig. 15. Tynet Burn, Banffshire, Scotland.

thin posterior flange (*p.f*) and a less-extensive, inflected postbranchial lamina (*la.pbr*). The base of the lateral surface is ornamented (*derm.l*, Text-fig. 40A; Miles 1966, Text-fig. 10), apparently because some body scales have fused with each other and with the girdle, to form a lateral dermal component. This lies immediately above the base of the pectoral spine, which is firmly attached to (perhaps overlapped by) the girdle, and it is not easy to decide exactly where the girdle and spine meet in articulate specimens. The postbranchial lamina may include part of the coracoid process, if this structure is not wholly represented by the procoracoid; ventrally it lies in contact with the anterior ridge of the posterior pinnal plate. In BM P.1364–P.4311 and RSM 1891.92.334 there is some indication that the base of the posterior flange of the scapula projects mesially, near the posterior margin, as a glenoid process (*gl.pr*). This is shown somewhat diagrammatically in Text-fig. 40B, and the incompletely ossified posterior surface of this process is represented as a margo radialis (*mr*). The determination of this process is supported by its position, immediately mesial to the base of the pectoral spine. If it is correct, it indicates that the scapula of *Diplacanthus* includes a perichondrally ossified region homologous with the dorsal part of the middle region in *Acanthodes*.

The procoracoid (*proco*, Text-figs 39A, 40A, 41) has been differently interpreted by Woodward (1891, 'infraclavicle') and Watson (1937, 'coracoid'; also Miles 1966). Woodward regarded it as a membrane bone, presumably because of its ornamentation, whereas Watson believed that it was an endoskeletal bone laid down round a cartilage, because of its calcite filling. The evidence of both of these workers is valid, and it is here interpreted to show that the perichondral procoracoid had a dermal element fused to its ventral surface. I have studied the bone by means of silicone-rubber replicas (Text-fig. 41), obtained by treating negatively prepared



Text-fig. 41. *Diplacanthus striatus* Agassiz. Middle Old Red Sandstone. Right procoracoid in A, ventral, B, lateral, and C, posterior views. After BM P.1364–4311 (counterparts). Tynet Burn, Banffshire, Scotland.

BM P.1364–4311 as a two-piece mould. The perichondral bone comprises a flat ventral lamina (*la.v*) with a high, dorsomesially directed process (*pr.dl*). The posterolateral face of the base of this process is hollowed into a distinct fossa (*psp.f*), which in the articulated girdle lies immediately in front of the basal opening of the first intermediate spine. The mesial margin of the ventral lamina lies in contact with the procoracoid of the other side, possibly in a butt-joint. Thus the two halves of the girdle are united in the middle line. The precise relationship of the procoracoid to the rest of the girdle is less easy to determine. Possibly the posterior margin of the ventral lamina abutted laterally against the base of the first intermediate spine, and it seems clear that the dorsal process rested in some way against the mesial edge of the postbranchial lamina of the scapula. Although the details of this last relationship are unknown, it is obvious that the connexion was not as highly evolved as in *Acanthodes*. It is germane to note, therefore, that the pectoral spine is fixed in *Diplacanthus*, and not mobile as in *Acanthodes*.

The dermal component (*derm.v*) is restricted to the mesial half of the lower face of the procoracoid (Text-fig. 41A). This element is paired and not easy to compare with the plates of climatioids. Topographically, both members of the pair might be compared with the median posterior lorical plate of *Climatius*, only this last plate is not associated with any part of the scapulocoracoid. An alternative comparison with one of the paired middle pinnal plate also founders, because these plates are laterally situated, in front of the posterior pinnal, and do not meet their fellows in the middle line. Therefore, I conclude that the dermal component of the procoracoid in *Diplacanthus* is a new element without a homologue in climatioids. It is comparable with the element attached to the lateral surface of the scapula, and was probably formed by the fusion of scales.

Pectoral fin. No remains of this structure have been found, apart from the 'ceratotrichia' figured by Watson (1937, Text-fig. 15, Pl. 10, fig. 1) in RSM 1891.92.334. Traquair's (1896, Pl. 2, fig. 1) restoration of the fin is, however, probably correct in principle.

Rhadinacanthus spp.

Traquair (1888 : 512) referred *Diplacanthus longispinus* Agassiz to the new genus *Rhadinacanthus*, because he believed it to lack 'the second or lower pair of intermediate spines' (i.e. the first intermediate spines). Woodward (1891 : 26), however, pointed out that these spines occur in their usual position in BM P.4041 from the Middle Old Red Sandstone of Gamrie. I have been able to confirm this in Woodward's specimen, and in other specimens from Scotland; and the spines can also be seen in the holotype (BM P.6756) of *Rhadinacanthus horridus* (Woodward) from the early Upper Devonian Escuminac Formation of Canada (Woodward 1892b; Russell 1951). Traquair (1896 : 244) appears to have accepted Woodward's point, but nevertheless retained the genus *Rhadinacanthus*. ('Distinguished by its long slender spines and its sharply and beautifully sculptured scales'.) On the evidence of the type species, *R. longispinus*, this genus can be most readily separated from *Diplacanthus* by the peculiar fact that the second dorsal fin-spine is longer than the first.[5] It is not yet possible to decide whether this is also true of *R. horridus* (cf. Woodward 1892b : 482; Russell 1951).

The shoulder-girdle is comparable in all respects in *Diplacanthus* spp. and *Rhadinacanthus* spp. Two comments only are required. In BM P.43276 (*R. longispinus*), from the Middle Old Red Sandstone of Tynet Burn, there are two small foramina on the inner face of the scapulocoracoid, which may together equal the subscapular foramen of *Acanthodes bronni*. They have been entered in the drawing of *Diplacanthus striatus* (*ff*, Text-fig. 20B). Russell (1951 : 405–406) writes that there is a 'restricted membrane joining lateral and admedian spines', but there is no evidence of a web between the pectoral and first intermediate spine in any acanthodian I have examined, and this statement may be wrong.

IV. THE EVOLUTION OF THE CLIMATIOID SHOULDER-GIRDLE

In the foregoing review of structure I have accepted that the paired fin-spines and the paired prepectoral and intermediate spines are serial homologues. Whether the median prepectoral spine represents an additional pair of elements in this series, which have come together in the middle line, is unknown, and it is not considered in this discussion. I have further hypothesised that there is fundamentally a one-to-one correspondence between the paired dermal plates and prepectoral spines in the shoulder-girdle. This segmentation is probably also expressed in the ventral part of the scapulocoracoid, in the form of vertical endochondral lamellae placed subtransversely across the cartilage of the girdle. At the moment, however, useful information about these lamellae is only found in *Climatius* and *Sabrinacanthus*, and an element of doubt remains about their significance. There is no evidence bearing on the exact segmental arrangement of the spines, other than their regular disposition in genera such as *Erriwacanthus* (Text-fig. 27).

From the one-to-one correspondence hypothesis of plates and paired spines it should follow that the posterior pinnal plate is more complex than I have so far indicated, as it is associated with both the pectoral and first intermediate spine. However, there is no evidence that it is a compound plate. I suggest, therefore, that the pectoral spine became displaced laterally (p. 207) before the (phylogenetic) formation of the dermal girdle, as it has this position in ischnacanthiforms and acanthodiforms, and that the first intermediate spine became displaced forwards and secondarily associated with the posterior pinnal plate as a subsequence to this event. The one-to-one correspondence hypothesis also implies that the primitive climatioid shoulder-girdle had a full set of prepectoral spines and well-developed dermal plates, and that these structures were reduced during the evolution of the group. This might be expected as the reduction of the exoskeleton is a general trend in the

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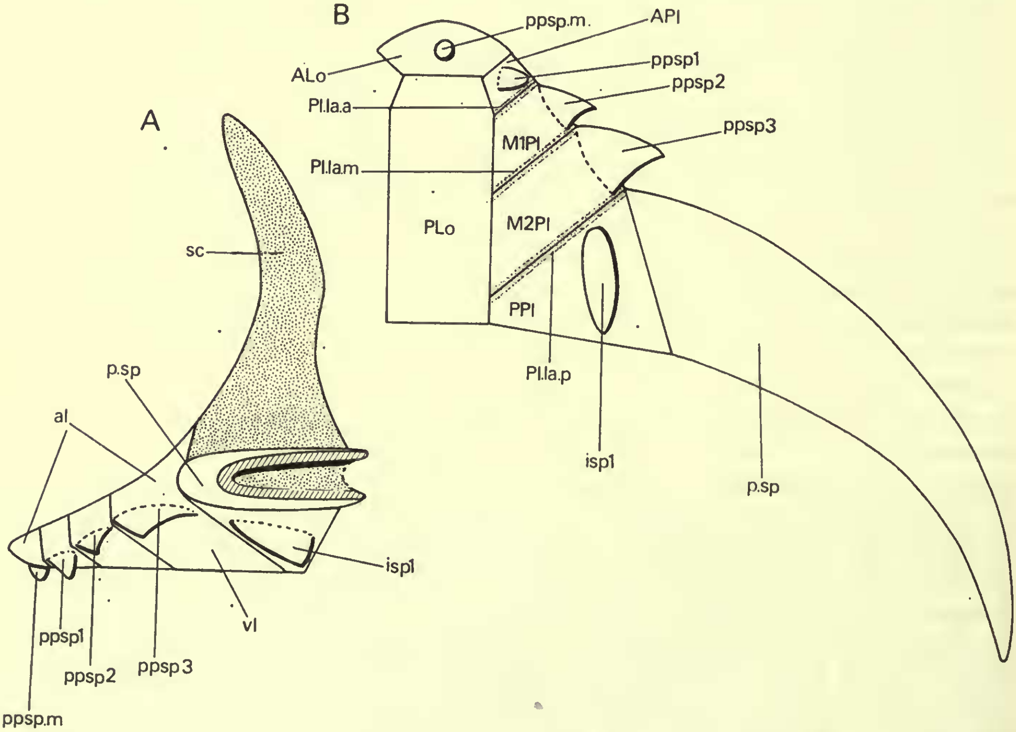
[5] I am indebted to Professor F. H. Stewart (pers. comm., Dec. 1964) for bringing this point to my notice.

evolution of many early groups of armoured fishes. The stratigraphical occurrence of climatioids does not weigh against this suggestion. There is evidence of up to three paired prepectoral spines, and this has been taken as the maximum number in the construction of a hypothetical primitive climatioid shoulder-girdle (Text-fig. 42). These spines are associated with the anterior, first and second middle pinnal plates; and the pectoral and first intermediate spines are associated with the posterior pinnal plate. I have also assumed that anterior and posterior lorical plates are present, and that the former is associated with the median prepectoral spine.

If the dermal shoulder-girdle of climatioids has evolved from a primitive structure of the type shown in Text-fig. 42, it is legitimate to seek interspecific homologies in the case of both the spines and plates. There is after all no reason to question the monophyly of climatioids. This stands in contrast to the problem of the intermediate spines. These are sets of homonomous (serially homologous) structures, but there are no ways of drawing safe interspecific homologies, except in the case of the first intermediate spine which is primitively included in the shoulder-girdle and normally retains an anterior position adjacent to the base of the pectoral spine. The remaining intermediate spines have been numbered separately in each species, with



TEXT-FIG. 42. Hypothetical primitive climatioid shoulder-girdle in A, lateral and B, ventral view. In A the scapulocoracoid is stippled and in B the positions of the internal endochondral lamellae are shown by bands of fine stipple.

the true first spine usually omitted from the counts (p. 164). Thus there are no means of demonstrating, e.g. that the second spine is homologous throughout climatioids. I might stress in passing that the 'first intermediate spine' of *Euthacanthus* (p. 184, Watson 1937, Text-fig. 4) stands some way behind the shoulder-girdle, and is almost certainly incorrectly determined.

The spines and dermal plates are variously reduced and lost among climatioids. I have concluded that a plate may persist following the loss of its spine (e.g. the anterior pinnal in *Brachyacanthus*, *Parexus* and *Vernicomacanthus*), but I have found no evidence of a prepectoral spine surviving after the loss of its pinnal plate, except in the poorly understood genus *Oracanthus*. This may be contrasted with the survival of the first intermediate spine (and pectoral spine) in the cited Old Red genera, following the loss of the posterior pinnal plate. The first intermediate spine appears, however, to have been completely suppressed among euthacanthids and gyracanthids.

It has proved difficult to determine the paired prepectoral spines in species in which they have been reduced from the primitive number of three. Paired prepectoral spine 3 seems generally to have been retained and as a rule is readily fixed. The reasons for other spine determinations have been given in the above accounts. Each case has been treated on its merits, but nevertheless the final results appear to be somewhat arbitrary. I have considered other interpretations, e.g. by applying the hypothesis that the paired prepectoral spines became reduced in a uniform sequence, such as in the order 2, 1, 3. But to my mind these have led to less convincing determinations than those presented in this paper.

A question quite distinct from the primitive extent of the exoskeletal shoulder-girdle concerns the primitive organization of this structure, particularly of its superficial layers. The exoskeleton of the pinnal plates described above exhibits four different states.

(1) The pinnal plates are fused together into a single structure with an undivided, ornamented surface (e.g. *Erriwacanthus falcatus*, *Sabrinacanthus*, *Vernicomacanthus*, *Parexus*).

(2) The pinnal plates are present as separate, thin, deeply-seated sheets of bone covered by mosaics of superficial, scale-like elements (*Climatius reticulatus;* see also comments on *Ptomacanthus anglicus*, p. 175).

(3) The pinnal plates are fused together basally into a single structure, but the superficial layer is divided into a mosaic of scale-like elements (*Erriwacanthus manbrookensis*).

(4) Discrete (including compound) pinnal plates are present, each with an undivided, ornamented surface (*Brachyacanthus*).

Erriwacanthus manbrookensis and *Brachyacanthus* are poorly known forms, and some doubt attaches to the exactness of paragraphs 3 and 4, particularly with respect to *Brachyacanthus*. The following discussion, therefore, is based on *Erriwacanthus falcatus* and *Climatius reticulatus*, and these species are judged to be sufficient for most of the points that have to be made. Both show primitive characters in the number of plates and prepectoral spines. *E. falcatus*, as far as it is known, cannot be separated from a hypothetical primitive climatioid (Text-fig. 42), whilst *C. reticulatus* differs only in the loss of paired prepectoral spine 2 and the first middle pinnal plate.

It is possible that the copinnal condition of *E. falcatus* is primitive, and that it was succeeded morphologically by a series of stages in which the copinnal became divided into separate pinnal plates, which were then reduced and lost in divers ways. However, it is also possible that the copinnal plate is found only in well grown individuals, and that younger specimens of *E. falcatus* had either separate, ornamented pinnal plates; or separate, deeply-seated, scale-covered pinnal plates as in *C. reticulatus*; or a compound basal plate with a divided superficial layer, as in *E. manbrookensis*. That is, the copinnal arose by bone fusions at a late stage of growth. Changes during growth of this nature are believed to have taken place in amphiaspid heterostracans (Obruchev 1967) and rhenanid placoderms (Westoll 1967 : 91). Indeed it is not impossible that *E. falcatus* passed successively through stages resembling *C. reticulatus* and *E. manbrookensis* during skeletogenesis. Ørvig (1967 : 139) regards the copinnal condition as probably 'a product of fusion' in phylogeny, and therefore as specialised relative to the condition in *C. reticulatus*, although he has not attempted to test this view. This hypothesis is unlikely in view of the general regressive evolution of the dermal skeleton in climatiiforms.

The condition of *C. reticulatus* with separate scale-like elements, apparently representing the superficial layers of the plates, has a parallel in rhenanid placoderms. In this group the tesserate condition has been regarded as primitive by Gross (1959), and as derived, by the regressive development of the armour, by Stensiö (1963). Westoll (1967 : 91–93), however, has argued that the mere fact of the existence of the tesserate condition gives no information about the direction of morphological change, which he attempted to deduce from a sequence of fossils. Westoll lists 'the development of separate thin tesserae, which may apparently become attached to underlying flanges of dermal bones' as one of 'several processes of dermal skeletogenesis in these forms'.

If the results of Westoll's analysis of skeletogenesis in rhenanids and psammosteid heterostracans are applied to *C. reticulatus* (and *E. manbrookensis*) they suggest that this species does not differ fundamentally from other climatioids in the tesserate condition of the exoskeleton, and cannot be said, without independent evidence, to be primitive or advanced in this character. It might be possible to compare the prepectoral–intermediate spines of the girdle with the raised centres of the plates on which the tesserae develop in psammosteids and rhenanids, and thus carry further the analogy between the development of the tesserae in these disparate groups.

The above discussion may be summarised as follows. *E. falcatus* and *C. reticulatus* are primitive climatioids in the shoulder-girdle because of the extent of the dermal skeleton and number of prepectoral spines. It is not possible definitely to say which is the more primitive in the form of the skeleton (as distinct from the number of plates and spines), or that either is more primitive in this respect than other Lower Devonian genera. The extrapolation of trends of change (*v.infra*) derived from other genera suggests, however, that a primitive adult condition is with a thick, compound pinnal plate, with an undivided, ornamented surface, and with two thick, ornamented lorical plates. *E. falcatus* may approach this condition closely. *E. manbrookensis* and *C. reticulatus* may be derived from this primitive condition either by deviation in skeletogenesis, or by bone reduction in the superficio-basal direction resulting in fragmentation; or either species may be at an antecedent stage and therefore still more primitive. With respect to the ornamented surface, I favour the first of these explanations, and it is interesting to recall in this connexion the growing body of evidence to suggest that there was a marked degree of morphological independence between the superficial and basal layers of the exoskeleton in ancient armoured fishes (Westoll 1967; Ørvig 1968). This explanation would also seem to account best for the differences in the basal layer of the skeleton.

The discernible tendencies in the evolution of the climatioid dermal shoulder-girdle may now be summarised. They are concerned with the reduction of the plates and spines, which seems very generally to have taken place in the following order:

(1) The loss of the posterior pinnal plate with the freeing of the pectoral and first intermediate spines.
(2) The loss of the posterior lorical plate.
(3) The loss of the ventral laminae of the anterior and middle pinnal plates.
(4) The loss of the anterior lorical plate and median prepectoral spine.
(5) The reduction of the ascending pinnal lamina and loss of paired prepectoral spines 1 and 2.
(6) The loss of the first intermediate spine.

Other than the pectoral spine, these changes result in the retention of the second middle pinnal and paired prepectoral spine 3 as the only dermal elements in euthacanthids, and the prepectoral spine alone among gyracanthids (*Oracanthus*). Their functional significance can best be explained by the assumption that they are correlated with the development of mobile pectoral spines (p. 207).

Some morphological relationships are worth noting. The posterior pinnal is related to the base of the coracoid, which it exactly matches in shape. The whole pinnal series (see e.g. the copinnal of *Erriwacanthus falcatus*) has a similar form and extent to the coracoid plus coracoid process (see e.g. *Sabrinacanthus*, *Ptomacanthus*), and primitively these areas of the exoskeleton and endoskeleton may have had a morphogenetic relationship, which can possibly be explained in terms of the Delamination Theory (Jarvik 1959). However, in ischnacanthiforms and acanthodiforms the coracoid and coracoid process (or procoracoid) developed in the absence of a dermal skeleton, and are readily comparable with the corresponding regions in climatioids. The posterior lorical lies under the pericardium and primitively may have protected the heart; and together with the anterior lorical it held the two halves of the girdle together rigidly. The protection of the heart may have been important in early genera which rested on the bottom, although acanthodians appear principally to have been a nektonic group. With respect to the second function it is possible that the loss of both the posterior lorical and posterior pinnal plates is correlated with the development of a mobile pectoral spine, and the acquisition of a less rigid girdle. The long coracoid processes of *Ptomacanthus* may well have been held together in the middle line by ligaments, as the median plates appear to be reduced in this genus (p. 175).

Erriwacanthus is wholly primitive in the characters it exhibits, and its relationships cannot be determined. Of the Scottish climatiids, *Climatius* is the most primitive genus and its nearest relative is undoubtedly *Brachyacanthus*. Although the features they share in the shoulder-girdle which are not found in the other genera (presence of a discrete posterior pinnal and possibly a posterior lorical) could both be interpreted as primitive, this relationship is supported by a far-reaching identity of structure in the head skeleton and body (Watson 1937). *Brachyacanthus* is specialised relative to *Climatius* in the loss of paired prepectoral spine 1, the apparent fusion of the anterior and second middle pinnal plates, and the reduction or loss of the posterior lorical; it is not known whether the median prepectoral spine was present.

A collateral line of descent to that of *Climatius* and *Brachyacanthus* among Scottish climatiids includes *Parexus* and *Vernicomacanthus* (*V. uncinatus*), although the common ancestor of these lines must have been more primitive than *Climatius* and possessed paired prepectoral spine 2. *Parexus* and *Vernicomacanthus* resemble each other in the loss of the ventral pinnal laminae and posterior lorical plate, and in the fusion of the ascending laminae of the anterior and first and second middle pinnal plates. It is possible that these resemblances are the result of parallel evolution from an *Erriwacanthus*-like common ancestor, but this possibility may reasonably be ignored till evidence is produced that demands its consideration. No such evidence is forthcoming from the shoulder-girdle or from the exoskeleton of the head.

The relationships of the English climatiids *Sabrinacanthus* and *Ptomacanthus* are less easy to determine, although I have some confidence in the hypothesis that *Ptomacanthus* belongs to the *Climatius-Brachyacanthus* side of the above division. *Ptomacanthus* resembles *Climatius* in the number and disposition of the prepectoral spines, in particular in the loss of paired spine 2 and the first middle pinnal plate, and in the scale-like condition of the ornamented surface of the remaining pinnal plates. The pinnal plates are, however, not discrete structures, and *Ptomacanthus* may be more advanced than *Climatius* and *Brachyacanthus* in the loss of the posterior lorical plate (and the first intermediate spine? See p. 122). I suggest that *Ptomacanthus* is more closely related to *Climatius* than to *Brachyacanthus*, but at the present time this cannot be tested.

Sabrinacanthus shows many primitive characters. It is advanced relative to a hypothetical primitive climatioid (Text-fig. 42), in the loss of paired prepectoral spine 1 and the corresponding anterior pinnal plate. This specialisation would be unexpected in the common ancestor of the two lines of Scottish genera considered above, and it suggests that *Sabrinacanthus* is equally distinct from both lines.

Euthacanthus resembles *Parexus* and *Vernicomacanthus* in the complete reduction of the posterior lorical plate and ventral pinnal laminae. *Euthacanthus* is more advanced than these genera, however, in the further loss of the anterior lorical, the median prepectoral spine and the anterior pinnal plate. It has also lost the first intermediate spine, this being a continuation of the trend which started with the loss of the posterior pinnal plate. Judged solely on the shoulder-girdle, it would be possible to regard *Euthacanthus* as more closely related to *Parexus* and *Vernicomacanthus* than to any other genera. This conclusion, if accepted, would demand some rearrangement of the existing classification, as at present *Euthacanthus* (Euthacanthidae) is placed apart from the Climatiidae. However, these groups differ notably from each other in the structure of the head, and for this reason I conclude that the similarities between *Euthacanthus* on the one hand and *Vernicomacanthus* and *Parexus* on the other, are the result of parallel evolution.

If *Gyracanthus* has been correctly interpreted, it is uniquely specialised in the reduction of the dermal girdle to a second middle-posterior pinnal plate with a ventral lamina and low ascending lamina behind the paired prepectoral spine (no. 3). It seems clear that the gyracanthids are more closely related to climatiids than they are to euthacanthids, but there is not enough information on which to base a discussion of their relationships. I maintain, therefore, their rank as a separate family.

V. COMPARISON BETWEEN CLIMATIOIDS AND DIPLACANTHOIDS

Diplacanthoids differ from climatioids such as *Climatius* and *Erriwacanthus* in the absence of prepectoral spines, the total reduction of the lorical plates (see p. 194), the reduction of the pinnal series to the posterior plate, and the hypertrophy of the first intermediate spine. Too few diplacanthoids are known for the evolutionary tendencies to be firmly established, but it is assumed that the dermal shoulder-girdle of a primitive diplacanthoid resembled that of a primitive climatioid in the presence of anterior pinnal, middle pinnal and lorical plates, and prepectoral spines. If so, diplacanthoids have paralleled climatioids in the reduction of the exoskeleton, but the changes have taken a different form, leading to the retention of the posterior pinnal plate rather than its loss, and to the suppression of the more anterior elements rather than their retention in some modified form.

The retention of the posterior pinnal may be correlated with the hypertrophy of the first intermediate spine, and not with the anchorage of the pectoral spine or the structure of the scapulocoracoid. It may be noted, however, that the posterior pinnal differs from that of climatioids in not extending mesially to the first intermediate spine.

The high scapular blade and strongly ribbed fin-spines are further characters in which climatioids and diplacanthoids resemble each other. Diplacanthoids are more advanced in the coracoid region, as they possess a separate procoracoid; and in this they have paralleled acanthodiforms and ischnacanthiforms. It is possible that there is a correlation in diplacanthoids between the possession of a procoracoid and the early loss of the anterior lorical and pinnal plates, particularly as there may be a phylogenetic (and ontogenetic?) connexion between the development of these plates and the coracoid process in primitive climatiiforms. I have suggested above that the dermal element attached to the procoracoid in diplacanthoids is a new structure that cannot be homologised with the pinnal or lorical plates.

This study of the shoulder-girdle strongly supports the current classification of climatiiforms into climatioids and diplacanthoids; this reflects a basic dichotomy of the group. However, Ørvig (1967 : 139), in an unexplained statement, has written that there appears to be more resemblance between diplacanthoids and *Erriwacanthus* (and *Climatius*) than between these genera and euthacanthids. He may be alluding to primitive characters.

VI. EVOLUTIONARY TENDENCIES IN ACANTHODIFORMS

The evolutionary tendencies in this group can be derived from the sequence *Mesacanthus* (Lower–Middle Devonian) – *Cheiracanthus* (Middle Devonian) – *Acanthodes* (Carboniferous–Lower Permian), assuming that the series arises in an hypothetical first term with a climatioid-like scapulocoracoid. They include:

(1) An increase in the ossification of the coracoid region.
(2) The division of the scapulocoracoid with the development of a separate procoracoid.
(3) The development of a moveable joint between the procoracoid and the scapulocoracoid.
(4) The development of a mobile pectoral spine.

These changes may be accompanied by the enlargement of the margo radialis; and the increased ossification of the coracoid region may indicate the development of more powerful fin muscles. It is unfortunate that *Mesacanthus* is poorly known, but the above statements are sustained by the conjecture that primitive acanthodiforms had fin articulation and fin muscle insertion areas of similar extent to those of the climatioid *Sabrinacanthus*. The coracoid process of climatioids can be homologised readily with the procoracoid of *Cheiracanthus* and *Acanthodes*. The joint between the procoracoid and scapulocoracoid corresponds in position with the posterior endochondral lamina of *Sabrinacanthus*.

The shoulder-girdle is still not well known in a sufficiently wide range of acanthodiforms for further conclusions to be drawn. But what is known appears to support the view that the division of this group into the Mesacanthidae, Cheiracanthidae and Acanthodidae results in a horizontal (grade) rather than a vertical (clade) classification (Miles 1966 : 174).

VII. THE INTERRELATIONSHIPS OF THE ACANTHODIAN ORDERS

It is regrettable that this study has not thrown more light on the problem of the interrelationships of the acanthodiforms, ischnacanthiforms and climatiiforms. The climatiiforms are the most distinct group, because of the presence of a dermal shoulder-girdle and prepectoral spines. It is likely that the extensive development of these structures is primitive for climatiiforms, but there is no good evidence that they are primitive for acanthodians as a whole. In particular there is no indication of their recent loss in the most primitive acanthodiforms and ischnacanthiforms. Acanthodiforms and ischnacanthiforms may thus resemble each other in the lack of these structures because (1) this is a shared primitive character, or (2) they have independently lost these structures, thus paralleling climatiiforms in the general reduction of the exoskeletal shoulder-girdle. In neither case would the explanation indicate a close relationship between the two groups. The third possibility, that the exoskeleton was lost in the common ancestors of these groups, cannot be demonstrated with the materials at hand. Some further, incomplete evidence is provided by the internal shoulder-girdle. A procoracoid is found in acanthodiforms, ischnacanthiforms and diplacanthoids, and although independently acquired it shows more resemblance in the first two groups than between either of these groups and the diplacanthoids. This may indicate the relative genetic affinity of these groups.

In view of the almost total lack of evidence bearing on the interrelationships of acanthodian orders, it is necessary to propose a tentative hypothesis that can be tested as more information becomes available on acanthodian structure. I suggest that the acanthodiforms and ischnacanthiforms shared a common ancestor more recently than either group shared a common ancestor with the climatiiforms. This hypothesis does not warrant any changes in the formal classification of acanthodians.

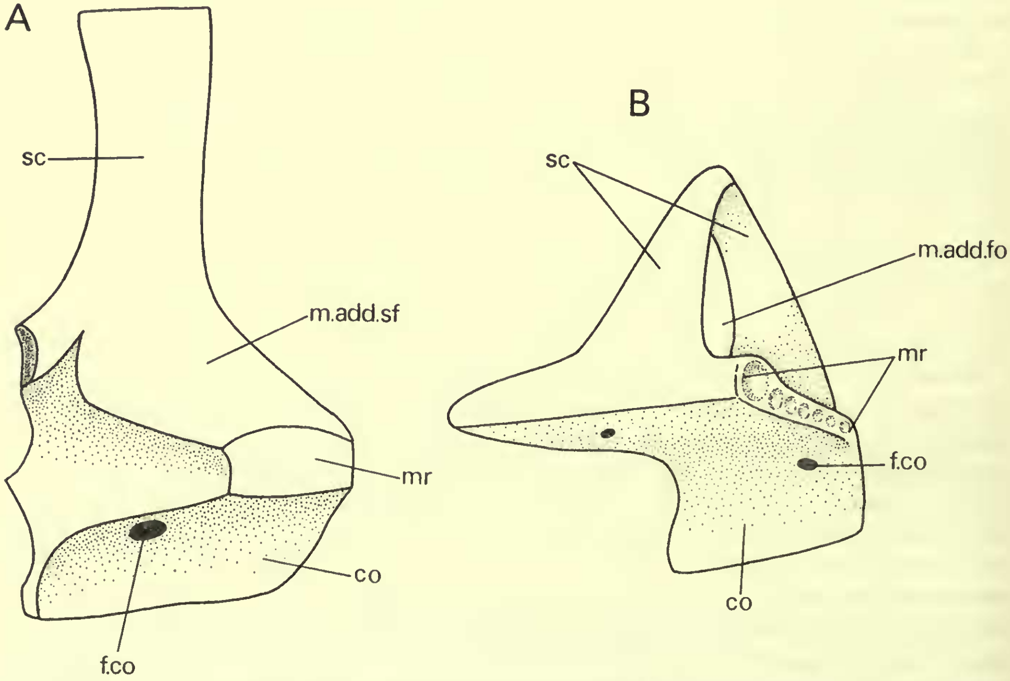
If this hypothesis is correct, the common possession of teeth by climatiiforms and ischnacanthiforms is probably a primitive character without phylogenetic significance. It is interesting to note, therefore, similarities in the dentitions of Upper Silurian species of these groups (Ørvig 1967), which suggest divergence from a primitive acanthodian type.

VIII. COMPARISONS WITH OTHER GROUPS OF FISHES

Scapulocoracoid

Romer (1924) has shown that the scapulocoracoid in primitive Recent osteichthyans (*Neoceratodus*, *Polypterus*, *Scaphirhynchus*, *Lepisosteus*, *Amia*) is of the same general type as in primitive tetrapods; and Andrews & Westoll (1970) have demonstrated that the scapulocoracoid of the rhipidistian *Eusthenopteron* is also of this type. These genera exhibit a coracoid plate, supraglenoid buttress (or mesocoracoid), supraglenoid and coracoid foramina, and areas for the origin of the dorsal and ventral fin muscles. The Recent genera also have distinct middle and scapular regions of the girdle. It is clear from the terminology used in the descriptions in this paper that *Acanthodes* closely matches this general type, having all the above characters, although it is specialised in the presence of a pectoral spine groove, procoracoid process, separate procoracoid and pectoral fossa (not found in climatioids). However, the significance of this general agreement is not clear, because the scapulocoracoid of chondrichthyans appears to be built on the same basic plan, with scapular and coracoid regions, and supraglenoid and coracoid foramina (Goodrich 1930: 164–165; Daniel 1934 : 79–81). It seems probable that Romer's work has established the basic type of gnathostome scapulocoracoid (but cf. placoderms, p. 205).

Despite the above conclusions, it seems worth while drawing attention to the close correspondence in structure between *Acanthodes* and palaeoniscoids such as *Pteronisculus* and *Moythomasia* (Nielsen 1942; Jessen 1968) and sturgeons (Sewertzoff 1926). The hollowed coracoid plate for the origin of the ventral muscles, and the broad, horizontal margo radialis are striking similarities (Text-fig. 43). The most important difference, apart from those involving the specialisations of *Acanthodes* listed above, is the absence of a dorsal muscle fossa in the base of the scapula in *Acanthodes*. However, if we now turn to the only other acanthodians in which the scapulocoracoid is well known, the climatioids *Sabrinacanthus* and *Ptomacanthus*, these similarities largely disappear, despite the absence in these genera of the specialisations associated with the mobile pectoral spine in *Acanthodes*. *Ptomacanthus* is close to elasmobranchs in the structure of the scapulocoracoid, particularly in the high, broad scapular blade, long coracoid process and apparent connexion with its fellow in the middle line. Xenacanth sharks, however, are said



Text-fig. 43. Comparison between the scapulocoracoid of A, *Acanthodes* (see Text-fig. 19) and B, a palaeoniscoid, *Moythomasia* cf. *striata*, Upper Devonian. B, after Jessen 1968, Text-fig. 7A. Both figures in approximately lateral view from left side.

to have unconnected scapulocoracoids, each with an 'infra-coracoidal' (and suprascapular) element (Goodrich 1930 : 164), and thus resemble *Acanthodes* rather than climatioids. A long coracoid process may be primitive for both acanthodians and chondrichthyans, and is also found in placoderms (Stensiö 1944, 1959). It is the site of origin of important hypobranchial muscles, and its reduction in acanthodiforms is the result of changes with a clear functional explanation (p. 202). The well developed scapular blade of *Ptomacanthus* is a character shared to some extent by all acanthodians, and among bony fishes by sturgeons (Severtzoff 1926, Text-fig. 10, 14; Goodrich 1930, Text-fig. 172; Jessen 1968, Text-fig. 7C, D). The significance of this blade in acanthodians and chondrichthyans lies in the absence of lateral, exoskeletal shoulder-girdle plates (Miles 1965 : 244); it serves to anchor the girdle in the body muscles and is a site for the origin of the superficial trapezius muscles. The extent of the scapular blade is, therefore, of doubtful phylogenetic significance, and this conclusion is reinforced by placoderms. In these elasmobranchiomorphs an exoskeletal 'shoulder-girdle' in the form of the trunk-shield is normally well developed, and the scapulocoracoid is a low structure without a scapular blade. The great differences between the scapulocoracoids of acanthodians and placoderms may be emphasised, because these groups have sometimes been classed together (Moy-Thomas 1939). The long, low scapulocoracoid of arthrodires appears basically to be crossed by a long series of diazonal nerves, each accompanied by a segmental artery and vein, and is difficult to compare with the basic adult gnathostome scapulocoracoid discussed above. Stensiö (1959) has had some success in interpreting it by comparison with the scapulocoracoids of shark embryos.

It may be concluded that the scapulocoracoid of acanthodians does not point decisively to either elasmobranch or teleostome relationships for this group, although it does corroborate the conclusion that they are not closely related to placoderms. The scapulocoracoid is probably close to the basic gnathostome type. It is unfortunate that the margo radialis is not more widely known, for the horizontal crest of *Acanthodes* is decidedly osteichthyan-like and there is some evidence that it has a similar form in *Sabrinacanthus*. In contrast, the glenoid of elasmobranchs seems normally to take the form of a knob or vertical depression in Recent species (Goodrich 1930; Daniel 1934; Smith 1937), and it may be like this or as an ill-defined lateral area (if the basal axis is in the body wall) in fossil forms (Schaeffer 1967, Text-fig. 1–6). Whether this similarity between acanthodians and early osteichthyans is dictated by function or propinquity of descent cannot yet be decided.

Dermal skeleton

Although scales may coat the outside of the scapulocoracoid, or fuse into a small plate as in diplacanthoids, there are no true, lateral exoskeletal shoulder-girdle bones in acanthodians. There are, however, ventral bones in climatiiforms, and it is possible to compare some of them with the bones of the osteichthyan girdle (Jarvik 1944) by virtue of their relationship to the pectoral fin and hind wall of the gill-chamber. Thus, using the hypothetical primitive climatioid pattern, the posterior pinnal may be compared with the ventral lamina of the cleithrum, the middle pinnals with the clavicle and the posterior lorical with the interclavicle. Yet it is obvious that the correspondence is not exact, and the comparison takes no account of the anterior lorical and pinnal plates. Other comparisons can be made taking these plates into account, with, for example, the boundary between the cleithral and clavicular regions drawn between the first and second middle pinnal plates, and the anterior lorical homologised with the interclavicle. But because of the imprecise nature of these comparisons, I am inclined to regard the ventral shoulder plates of acanthodians and osteichthyans as independently acquired structures, and the similarities between them as fortuitous. In favour of this view is the conclusion that most of the plates (not the posterior lorical) in climatiiforms are related to a prepectoral or intermediate spine. Such spines are not found in osteichthyans. Nevertheless, the independent development of similar shoulder-girdle plates in acanthodians and osteichthyans might be due to the inheritance of a common genetic potential.

A similar comparison can be made between climatiiform plates and the ventral plates of the trunk-shield in placoderms. But this comparison is far fetched and even less convincing than the comparison with osteichthyans. It may be true that the pectoral spine of placoderms is formed primitively around a lateral prepectoral process of the scapulocoracoid, like the fin-spine of a primitive acanthodian. Nevertheless, I believe it is entirely coincidental that the posterior pinnal of *Diplacanthus* attaches to the pectoral spine in the same way that the anterior ventrolateral plate clasps the spinal plate in placoderms (cf. Watson 1937 : 132).

Westoll (1967 : 97) has suggested that 'the scapular blade of elasmobranchs and of tetrapods may be a development from dermal shoulder-girdle elements', by the operation of delamination during phylogeny. There is no evidence that this is the explanation of the prominent scapular blade in primitive acanthodians, and if one concludes that acanthodians have never had an osteichthyan type of dermal shoulder girdle or placoderm-like trunk-shield, this explanation cannot be applied. The internal and external shoulder-girdles of fishes probably had separate origins (Jarvik 1965 : 152). It is not possible to say which arose first in a general statement framed to cover all groups, but in placoderms and osteichythans it is normally the dermal girdle and in acanthodians and chondrichthyans the endoskeletal girdle which is prominently developed.

Pectoral fin

In view of the often repeated, incorrect statement that the intermediate spines of acanthodians carried fins, it is necessary to stress that none of the prepectoral-intermediate spines in climatiiforms was equipped with a web, and that the pectoral fin was the only fin that articulated with the girdle. The pelvic, intermediate and prepectoral spines form a single, paired series in a ventrolateral line of potential fin development along the body (Westoll 1958; 'ventrolateral crest', Jarvik 1965). From Text-figs 25, 27, and the restorations of Watson (1937, Text-figs 2B, 4) and

Ørvig (1967, Text-fig. 2), it is obvious that the pectoral fin-spine lies outside this series. Nevertheless it probably arose in the same line as the other spines, and has been secondarily displaced laterally together with the base of the fin, either for hydrodynamic reasons or because of the size of the web. I cannot accept an alternative explanation which supposes that there were laterally two lines of potential fin development, although Ørvig (1961 : 517, footnote) has suggested that there may be structures representing two or more pairs of lateral 'potential fin-folds' in certain agnathans.

The skeleton of the pectoral fin is only well known in *Acanthodes bronni*, in which I have interpreted it as actinopterygian-like (p. 153), in contrast to Watson (1937) who regarded it as forming a tribasal structure of elasmobranch type. The 'ceratotrichia' and lepidotrichia-like rows of scales in acanthodians have been discussed elsewhere (Miles 1970 : 358); they permit no phylogenetic conclusions to be drawn. The presence of fin scales in some Lower Devonian climatioids indicates that the pectoral fin had a large, well-developed web and a short base, in the earliest articulated species. It now seems clear that the fins were more than mere 'thick, fleshy fin-folds' (Westoll 1945, 1958), and this is supported by the presence of an *Acanthodes* type of internal skeleton in the Lower Devonian species *Ischnacanthus gracilis*.

Clear trends of change can be seen in the pectoral spines (Westoll 1945, 1958). An instructive morphological series comprises a climatiid (e.g. *Ptomacanthus*) – *Mesacanthus* – *Cheiracanthus* – *Acanthodes*. These forms show a progressive change from a short, coarsely ornamented spine firmly fixed to the scapulocoracoid, to a long, slender, smooth spine moveably articulated and capable of erection. These changes are possibly correlated with the reduction of the intermediate spines. It is not possible to say definitely whether they are paralleled in ischnacanthiforms and climatioids, but this is likely, and if they are they explain the reduction of the exoskeletal girdle in climatioids.

The pectoral spines of advanced acanthodiforms invite comparisons with the analogous pectoral spines of sturgeons and catfishes, which are formed from hypertrophied lepidotrichia. Jarvik (1965 : 151, Text-figs 5E, F, 10D) has touched on this subject, and has figured a young *Acipenser ruthenus* which clearly shows the position of the pectoral spine lateral to the ventrolateral crest, like the pectoral spine of acanthodians. It is, perhaps, remarkable that analogous spines have not been produced in chondrichthyans, despite the presence of scales on the fin. This might have a functional explanation; it may reflect differences in the inherited evolutionary potential of chondrichthyans and teleostomes; or the difference may be purely aleatory.

In addition to their hydrodynamic significance, the pectoral spines of catfishes have a protective function (Alexander 1965), and probably this is also true of acanthodians. A fish with erect spines is more difficult for a predator to swallow whole, although for the spines to be effective they must also be firmly held in position so that they are not depressed by the predator's jaws. Whilst it is clear that the pectoral spines could be erected in *Acanthodes*, there is no indication of a locking mechanism (cf. catfishes; Alexander 1965). This may, therefore, have been muscular, relying on the same muscles that were used to erect and depress the spine (p. 155). It is possible that the ventral dermal plates of climatiiforms were initially evolved to give a firm mounting for the pectoral and associated spines. However, this explanation makes it difficult to understand the early reduction of the posterior pinnal plate and freeing of the pectoral and first intermediate spines in climatioids, unless the pectoral spine became mobile and was provided with a muscular locking mechanism. The fixedness of the pectoral spines of primitive climatiiforms may be correlated with their short length, but if this is so, it suggests that at least the long pectoral spines of gyracanthids were mobile. In acanthodiforms the dorsal, pelvic and intermediate spines are reduced as the pectorals become elongated and more mobile, and therefore more efficient defences, and these changes may have been paralleled to some extent in the gyracanthids.

This study has produced no compelling evidence on the relationships of acanthodians to elasmobranchs and osteichthyans, but it confirms that they are not closely related to placoderms and does not deny the osteichthyan affinities suggested by the study of cranial structures. The skeleton of the pectoral fin and the form of the margo radialis are consistent with this view. I hold, therefore, to my earlier conclusion that acanthodians are a line of teleostomes collateral with the osteichthyans.

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X. ABBREVIATIONS USED IN FIGURES

ALo	anterior lorical plate
AM1,2Pl	anterior – first middle – second middle pinnal plate
AM2Pl	anterior – second middle pinnal plate
APl	anterior pinnal plate
CPl	copinnal plate
Ha	anterior elements in dorsal region of hyoid gill-cover
Hp	posterior elements in dorsal region of hyoid gill-cover
Lo	lorical plate
M1Pl	first middle pinnal plate
M2Pl	second middle pinnal plate
M1,2PPl	first middle – second middle – posterior pinnal plate
Pl.la.a	anterior endochondral lamina
Pl.la.m	middle endochondral lamina
Pl.la.p	posterior endochondral lamina
PLo	posterior lorical plate
PPl	posterior pinnal plate
V3	notch for ramus mandibularis trigemini
Z1–Z4	scale zones of caudal fin (explained in text)
Ia–IVa	anterior dermal elements in gill-covers 1 to 4
Ip–IVp	posterior dermal elements in gill-covers 1 to 4
Ivt	ventral tesserae of gill-cover 1
ad.sp	anterior dorsal spine
al	ascending lamina
a.sp	anal spine
bpl	basal plate of tooth
br	branchiostegal ray
br.a	anterior exoskeletal elements of gill-arches
br.p	posterior exoskeletal elements of gill-arches
cart(mr)	cartilaginous region around margo radialis
cav.p.sp	cavity of pectoral spine
cav.sp	cavity of prepectoral-intermediate spine
ch.edg	bevelled edge of pinnal plate
cmo	circumorbital plates
co	coracoid
cp	tooth cusp
cr.epq	extrapalatoquadrate ridge
dc	dorsal sensory commissure
derm.l	lateral dermal plate
derm.v	ventral dermal plate
dg.b	dentigerous bone
dmf	dorsal muscle fossa
dnvc	dorsal neurovascular canals
dp.pe	pericardial depression
end	endolymphatic duct
f.add	adductor fossa
f.co	coracoid foramen
ff	foramina on inner face of scapula
fo.p	pectoral fossa
fo.sbsc	subscapular fossa
gcl	gill-clefts
gl.pr	glenoid process
hgf	hyoid gill-flap
inf.ot	otic branch of infraorbital sensory-line
isp 1–6	intermediate spines 1 to 6
jut	juglar tesserae
la.l	lateral lamina of pinnal plate
la.pbr	postbranchial lamina of pinnal plate
las	labial surface of tooth
la.v	ventral lamina of procoracoid
lj.t	lower jaw teeth
ll	main lateral-line
m.add.fo	fossa for adductor muscles
m.add.sf	surface for origin of adductor muscles
mk	meckelian cartilage
mk.a	mentomandibular
mk.p	articular
mr	margo radialis
na	external nasal opening
nt	navicular tesserae
pbpr	prebranchial projection
p.f	posterior flange of scapula
pfc	'profundus' sensory-line
p.gr	pectoral groove (for pectoral spine)
poc	preopercular sensory-line
popr	postorbital projection
ppsp 1–3	paired prepectoral spines 1 to 3
ppsp.m	median prepectoral spine
pq	palatoquadrate
pr.art	articular process
pr.preart	prearticular process
pr.co	coracoid process
proco	procoracoid
pr.pregl	preglenoid process
pr.d	dorsal posterior process of procoracoid
pr.dl	dorsal process of procoracoid

pr.proco	procoracoid process of scapulocoracoid
pr.v	ventral posterior process of procoracoid
p.sp	pectoral spine
p.sp.cf	contact face for pectoral spine
psp.f	fossa for pectoral spine
pv.f	pelvic fin
pv.sp	pelvic spine
ra	radial
rdg	ridge down scapula
rdg.a	anterior ridge of posterior pinnal plate
rdg.p	posterior ridge of posterior pinnal plate
rdg.pcav	ridge posterior to opening of prepectoral spine
rdg.Pl	ridge around mesial region of posterior pinnal plate
rdg.ppsp	ridges on leading face of prepectoral spine
sc	scapula
scco	scapulocoracoid
sc.oa	scapular overlap area
scp	side cusp
shg	shoulder-girdle
sml	supramaxillary sensory-line
soc	supraorbital sensory-line
sqt	squamosal tesserae
ssc	suprascapula
t	teeth
tgu	gular tesserae
tt	tectal tesserae
uj.t	upper jaw teeth
vl	ventral lamina
vmf	ventral muscle fossa
vnvc	ventral neurovascular canals
vll	ventral lateral-line

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London SW7 5BD

PLATE 1

Vernicomacanthus waynensis gen. et sp. nov.

Fig. 1. Cast of holotype, BM P.24938a. Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Newton, Herefordshire, England.

Ptomacanthus anglicus gen. et sp. nov.

Fig. 2. Cast of holotype, BM P.19999. Horizon and locality as for fig. 1.

Vernicomacanthus waynensis gen. et sp. nov.

Fig. 3. Cast of holotype, BM P.24938a. Detail of flank scales. Horizon and locality as for fig. 1.

Photos: T. W. Parmenter.

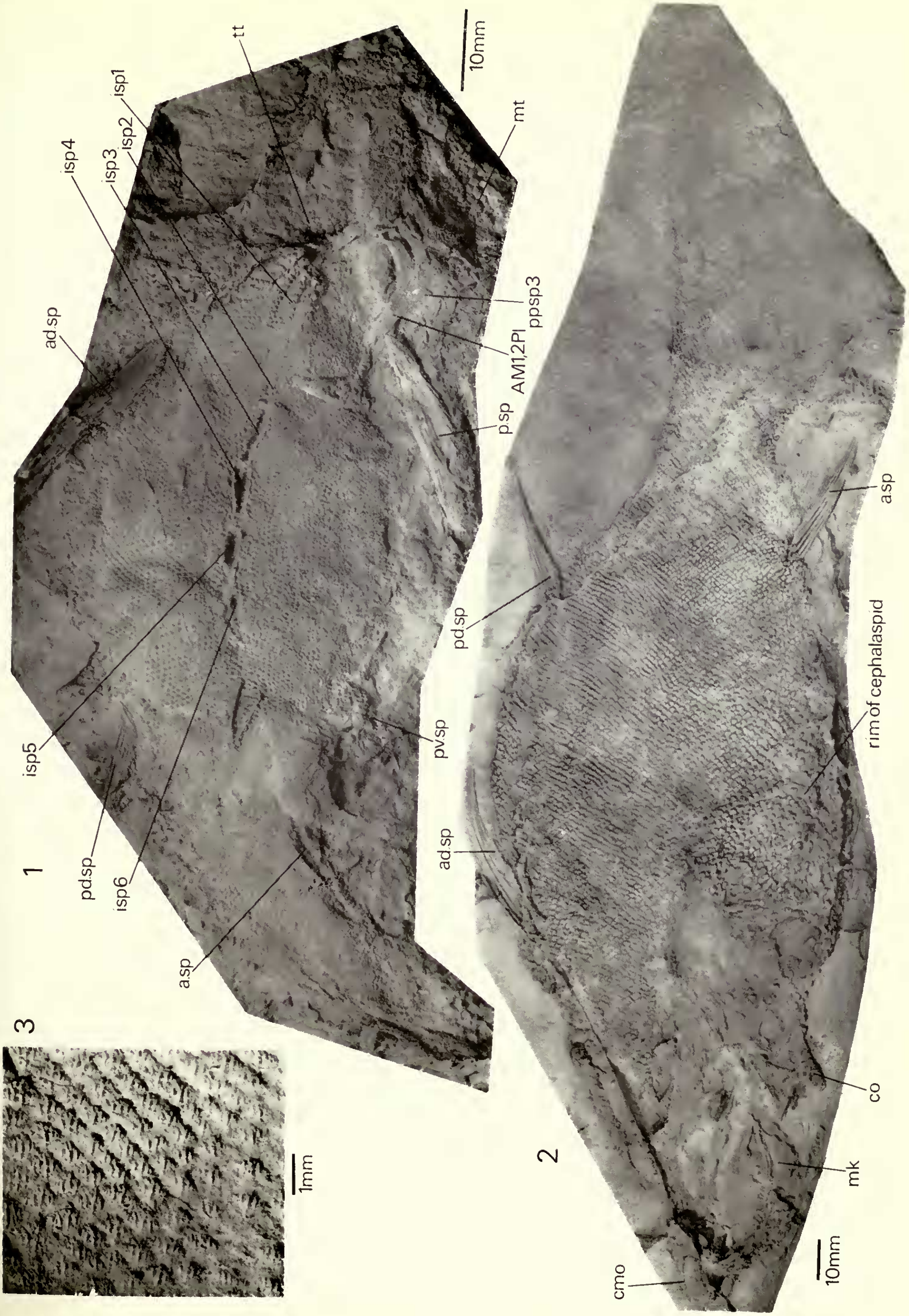

1
tt
isp1
isp2
isp3
isp4
10mm
mt
ppsp3
AM1,2Pl
ad.sp
p.sp
isp5
pd.sp
isp6
pv.sp
a.sp
2
pd.sp
a.sp
rim of cephalaspid
ad.sp
co
mk
cmo
10mm
3
1mm

PLATE 2

Climatius reticulatus Agassiz

Head of BM P.1343. Use Text-fig. 5 as key-diagram. Arbuthnott Group, Dundee Formation, Lower Old Red Sandstone, Turin Hill, Angus, Scotland.

Photo: Tordis Junker.


5mm

PLATE 3

Climatius reticulatus Agassiz

Right jaw cartilages, teeth and part of left shoulder-girdle. GSM 49785 Arbuthnott Group, Dundee Formation, Lower and Red Sandstone, Turin Hill, Angus, Scotland. In alcohol.

Photo: T. W. Parmenter.

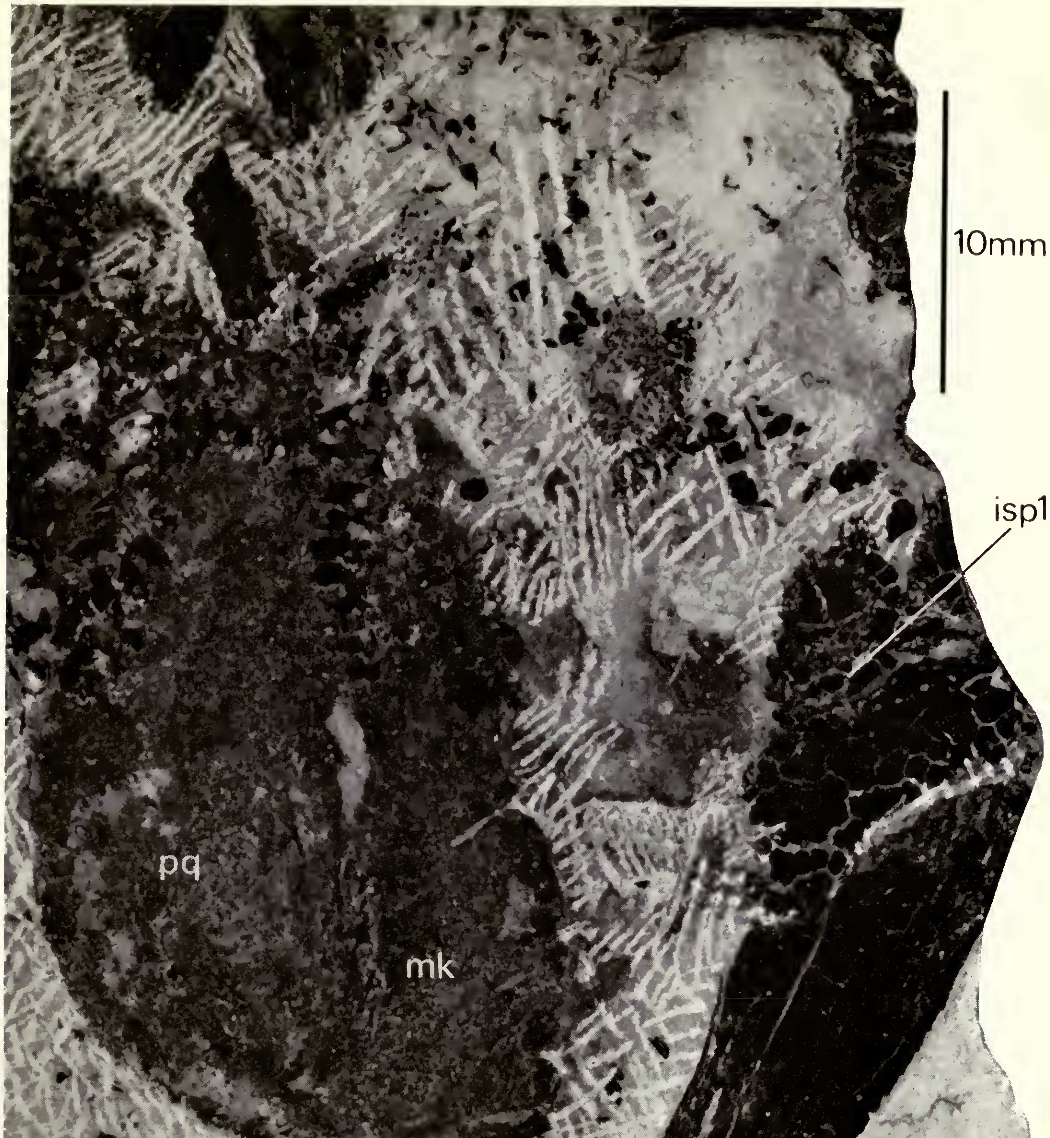

10mm
isp1
pq
mk

PLATE 4

Ptomacanthus anglicus gen. et sp. nov.

Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Newton, Herefordshire, England.

FIG. 1. Cast of holotype, BM P.19999. Detail of palatoquadrate and meckelian cartilage. Use Text-fig. 12 as key-diagram.

FIG. 2. Cast of BM P.20003. Detail of shoulder-girdle. Use Text-fig. 4 as key-diagram.

Photos: T. W. Parmenter.

1

2

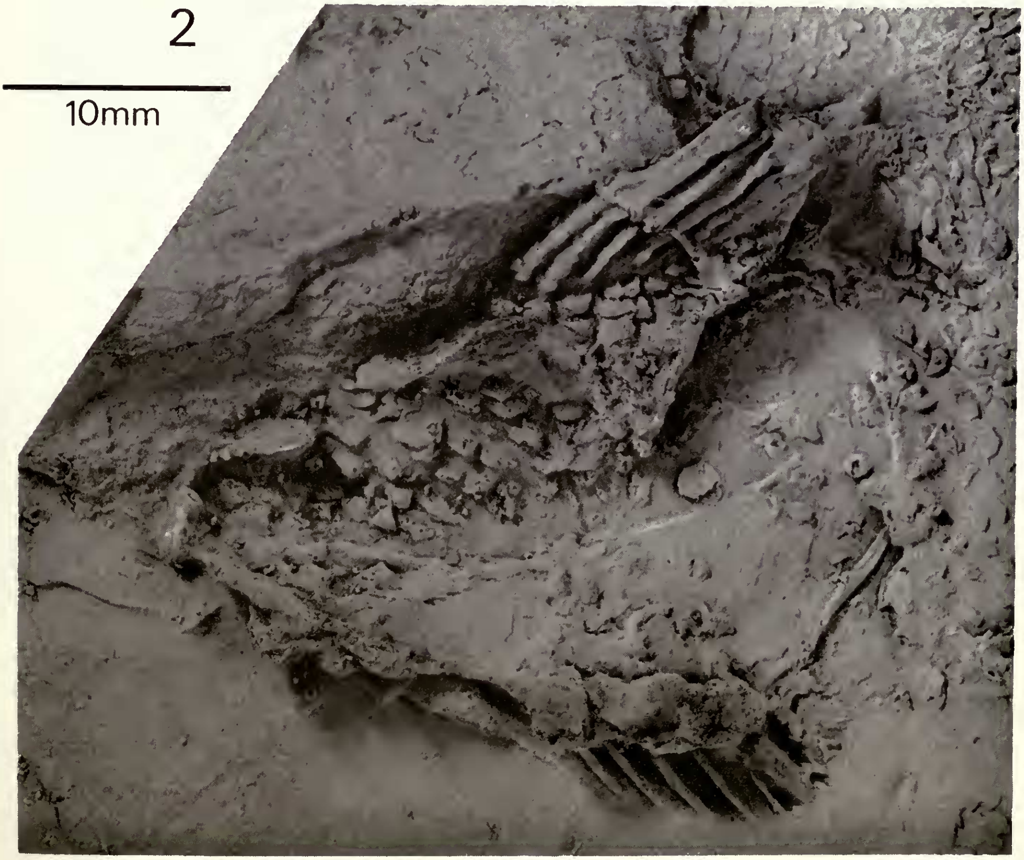


PLATE 5

Ptomacanthus anglicus gen. et sp. nov.

Flattened head in dorsal view. Cast of BM P.24919b. Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Newton, Herefordshire, England.

Photo: T. W. Parmenter.

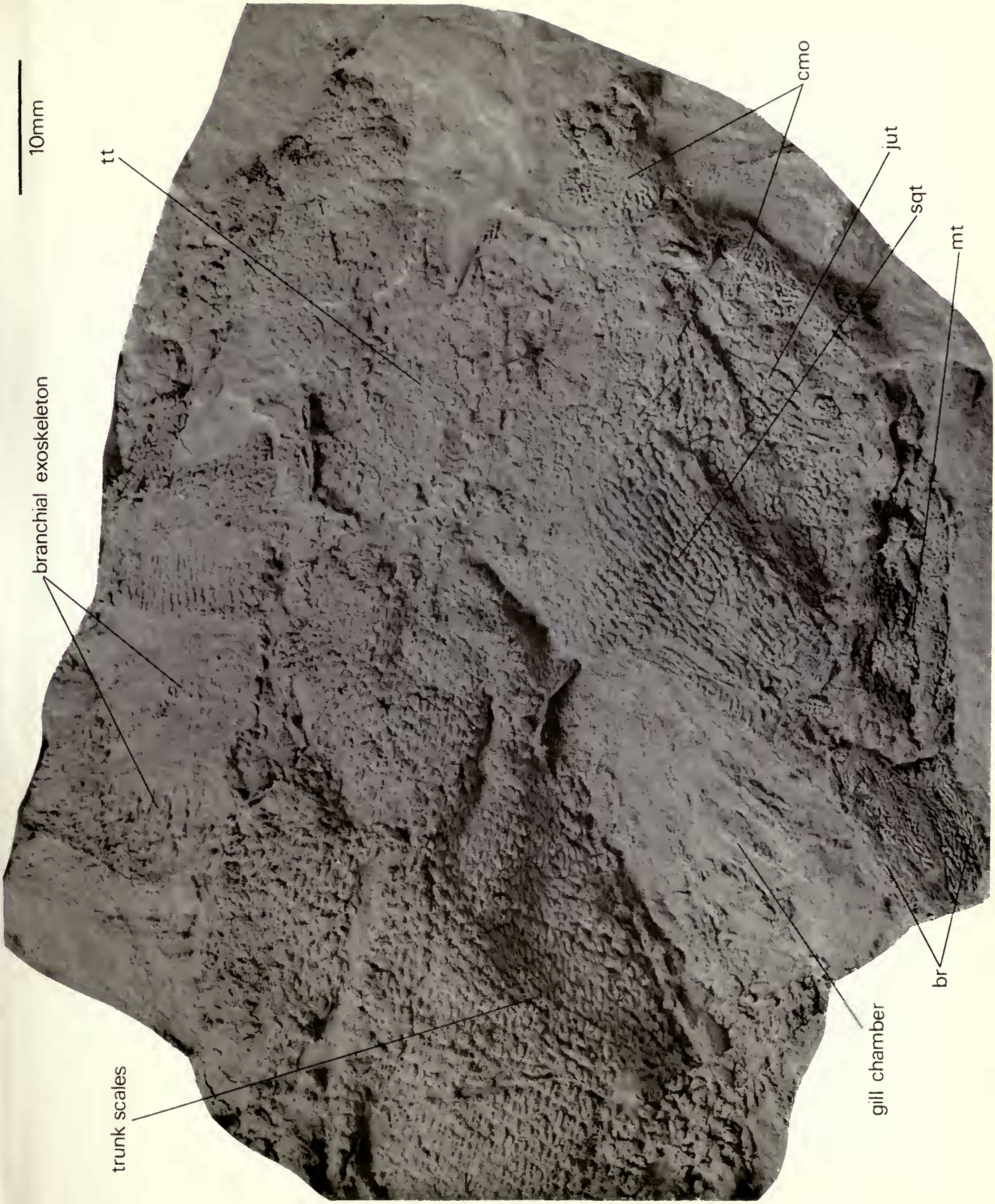

10mm
tt
branchial exoskeleton
trunk scales
cmo
jut
sqt
mt
br
gill chamber

PLATE 6

Ptomacanthus anglicus gen. et sp. nov.

Flattened head in ventral view with upper dentition *in situ*. Cast of BM P.24919a. Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Newton, Herefordshire, England.

Photo: T. W. Parmenter.


exoskeleton of snout
endoskeleton
teeth
pq
tt
br.a
br.p
na
row of tesserae interlocking with anterior teeth
10mm
pq
sqt
tgu
mkp
br

PLATE 7

Vernicomacanthus gen. nov. ***uncinatus*** (Powrie)

Skull-roof, right cheek and shoulder-girdle in dorsal view. RSM Kinnaird collection 82. Arbuthnott Group, Dundee Formation, Lower Old Red Sandstone, Turin Hill, Angus, Scotland.

Photo: R. C. M. Thomson.

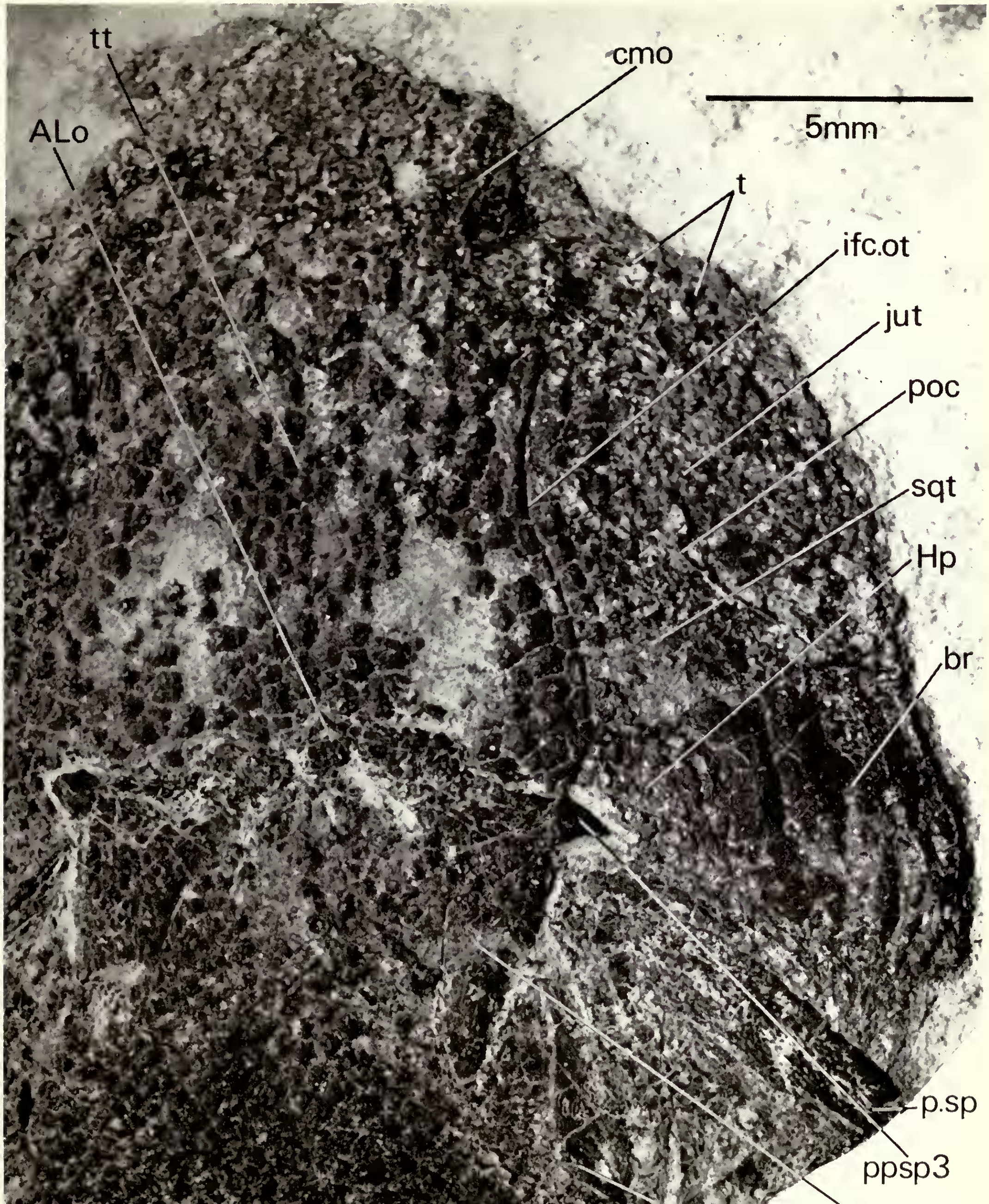

tt
cmo
ALo
5mm
t
ifc.ot
jut
poc
sqt
Hp
br
p.sp
ppsp3
AM1,2Pl(al)
isp1
sc

PLATE 8

Vernicomacanthus waynensis gen. et sp. nov.

Cast of holotype, BM P.24938b. Counterpart of specimen in Pl. 1, fig. 1. Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Newton, Herefordshire, England.

Photo: T. W. Parmenter.

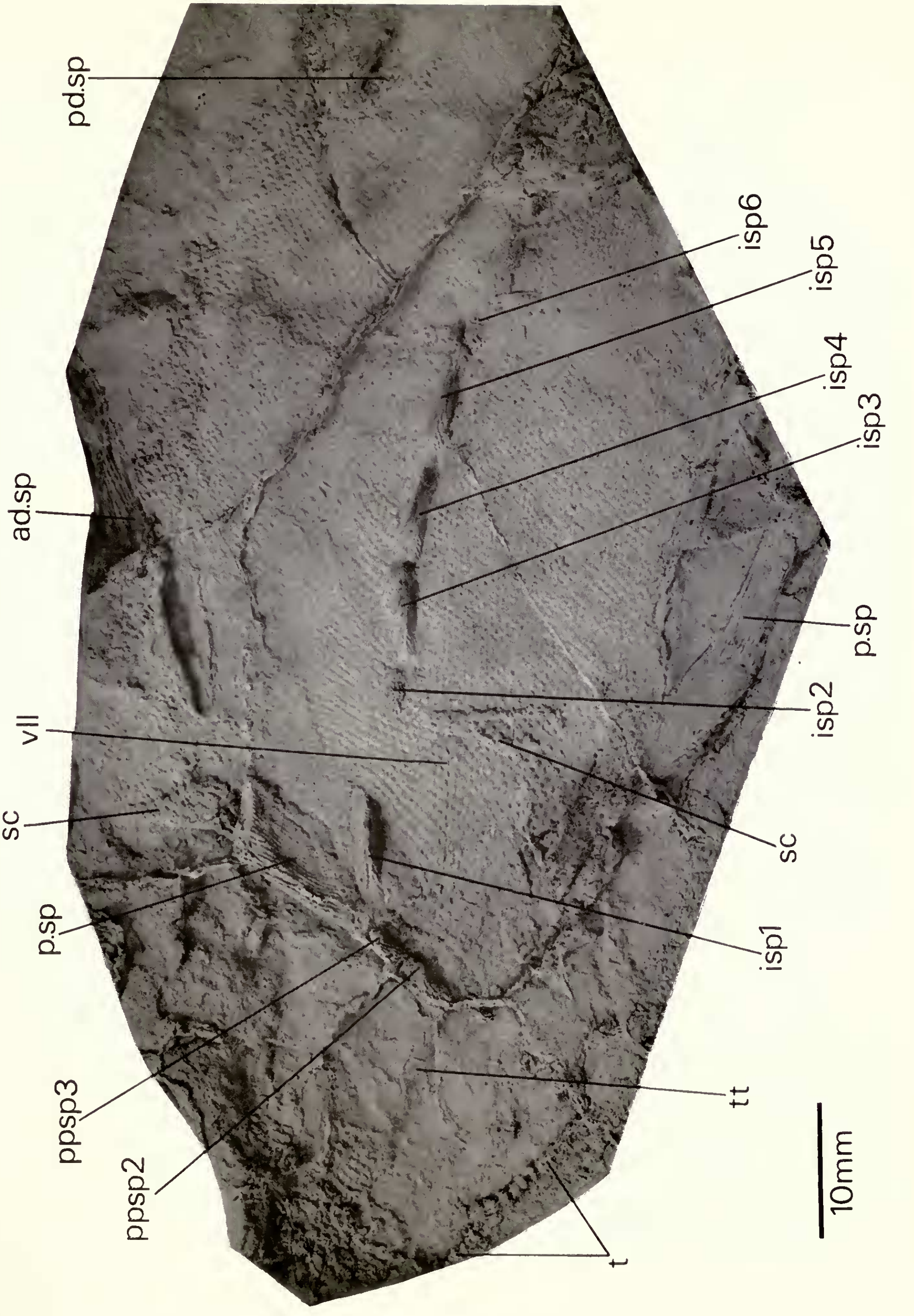

pd.sp
ad.sp
vII
sc
p.sp
ppsp3
ppsp2
isp6
isp5
isp4
isp3
p.sp
isp2
sc
isp1
tt
t
10mm

PLATE 9

Vernicomacanthus waynensis gen. et sp. nov.

Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Newton, Herefordshire, England.

Fig. 1. Cast of BM P.52441a. Detail of ventral surface in pelvic region.

Fig. 2. Cast of holotype, BM P.24938b. Detail of head and shoulder-girdle from same cast as in Pl. 8.

Photos: T. W. Parmenter.

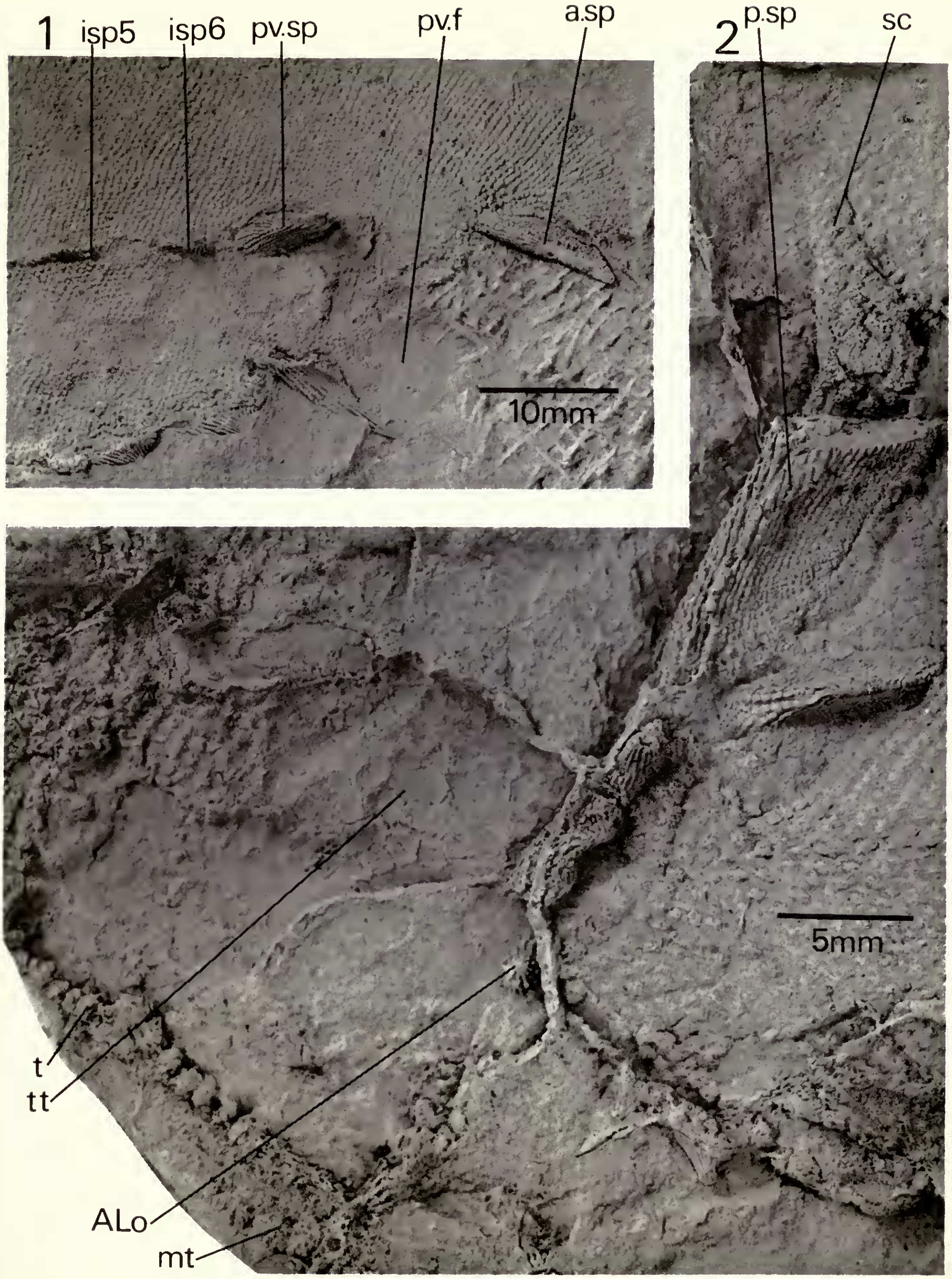

1
isp5
isp6
pv.sp
pv.f
a.sp
10mm
2
p.sp
sc
5mm
t
tt
ALo
mt

PLATE 10

Vernicomacanthus waynensis gen. et sp. nov.

Cast of BM P.52441b. Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Newton, Herefordshire, England.

Photo: T. W. Parmenter.

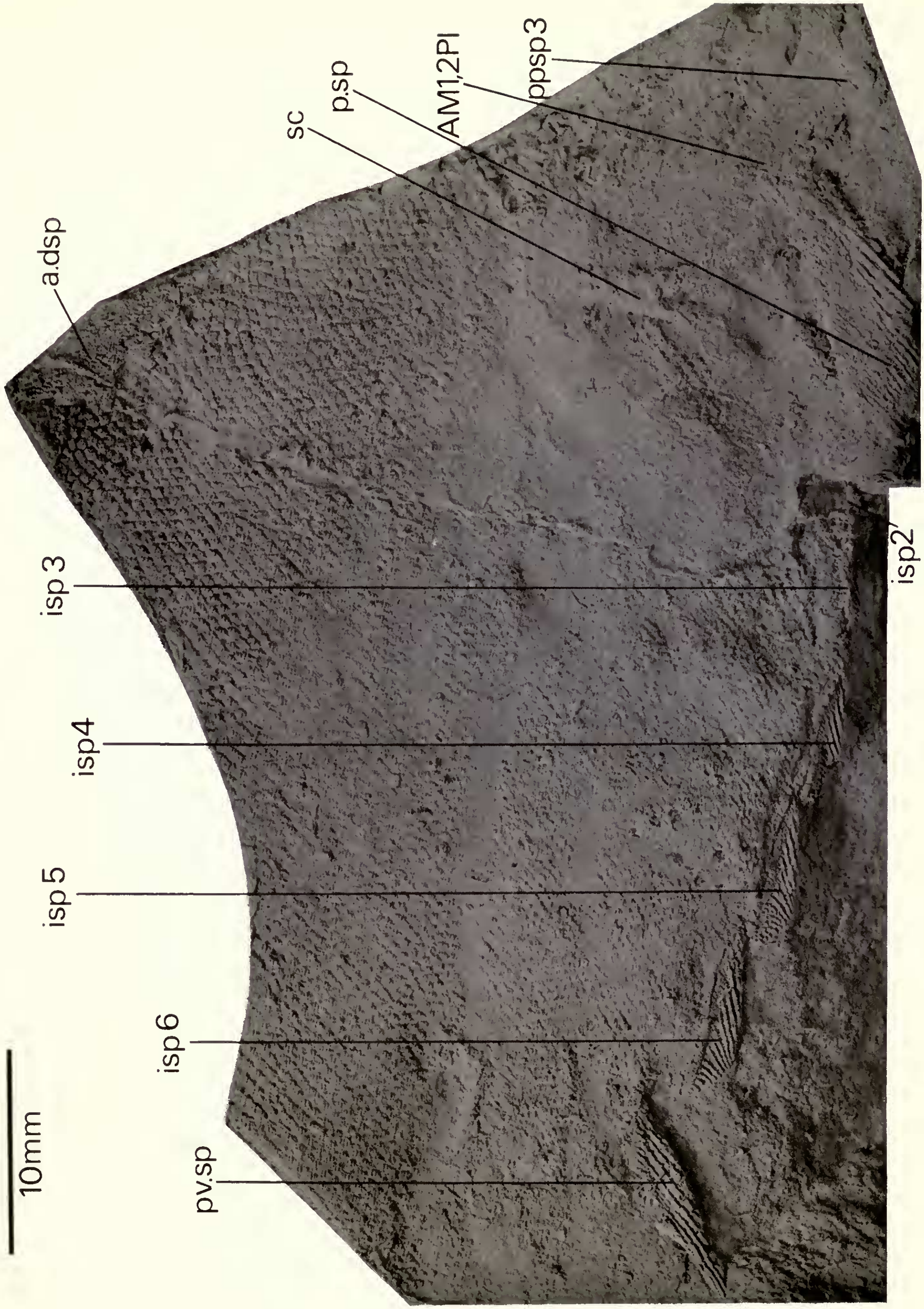

a.dsp
sc
p.sp
AM1,2Pl
ppsp3
isp 3
isp2'
isp4
isp 5
isp6
pv.sp
10mm

PLATE 11

Uraniacanthus spinosus gen. et sp. nov.

Cast of holotype, BM P.16609. Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Newton, Herefordshire, England.

Photo: T. W. Parmenter.

PLATE 11

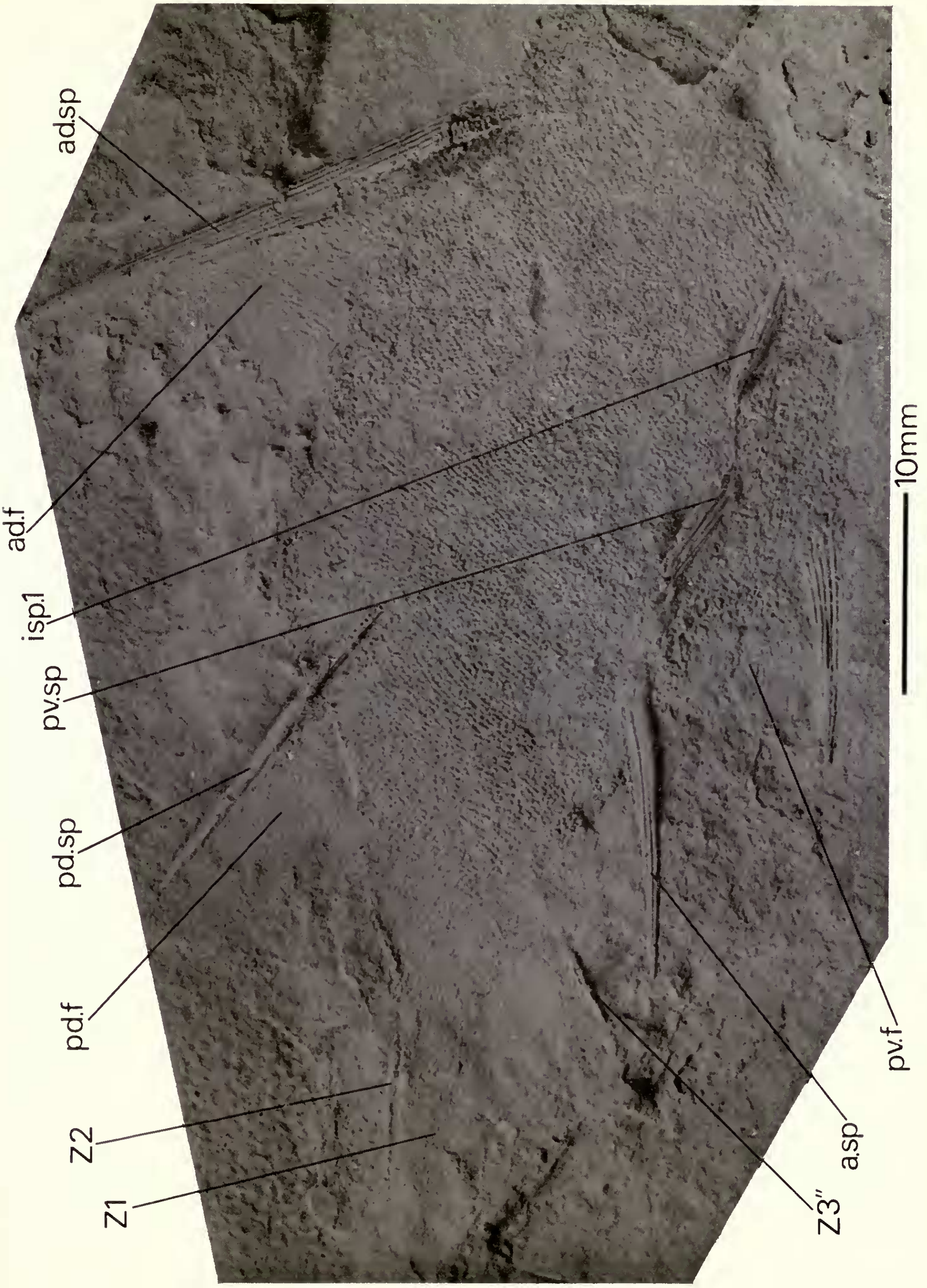


PLATE 12

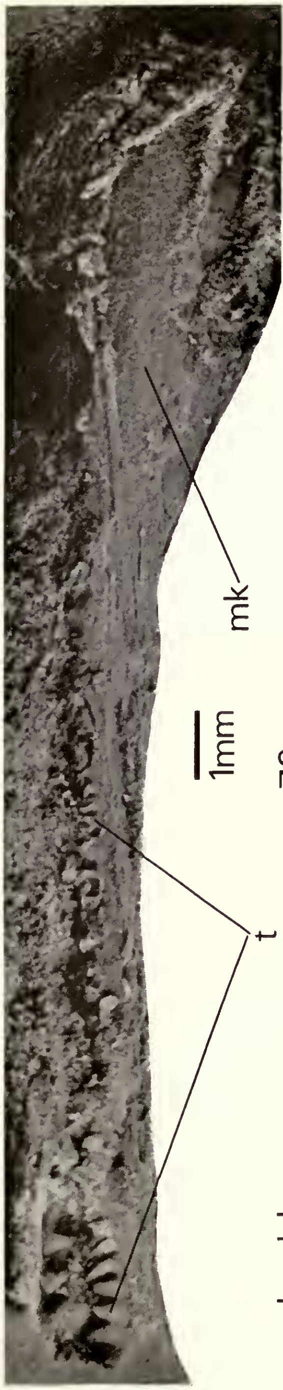
Uraniacanthus spinosus gen. et sp. nov.

Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Newton, Herefordshire, England.

Fig. 1. Cast of BM P.53032. Incomplete jaws and teeth. Photo: Dr R. P. S. Jefferies.

Fig. 2. BM P.20001. Posterior part of body. Photo: T. W. Parmenter.

1



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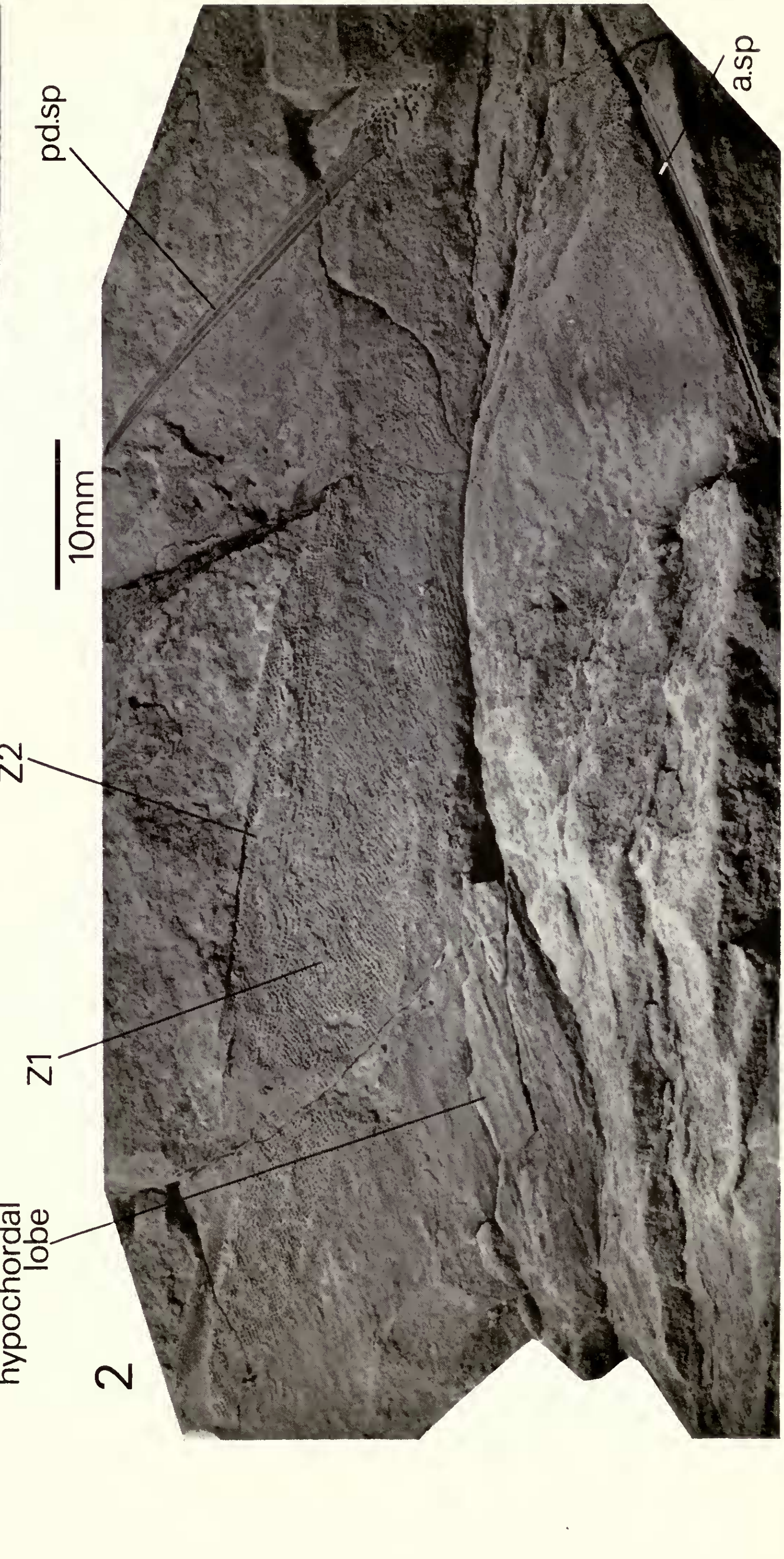


PLATE 13

Uraniacanthus spinosus gen. et sp. nov.

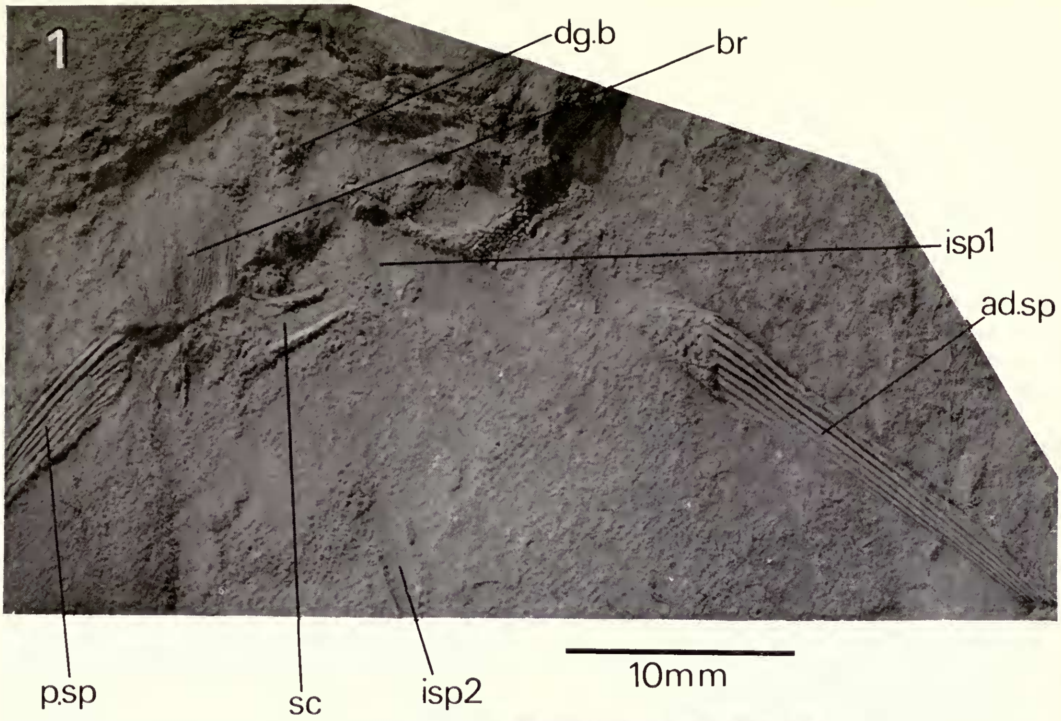
Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Herefordshire, England.

Fig. 1. Cast of BM P.16612. Head and shoulder-girdle in dorsal view.

Fig. 2. Cast of BM P.16613. Counterpart of P.16612. Head and shoulder-girdle in ventral view.

Photos: T. W. Parmenter.

1



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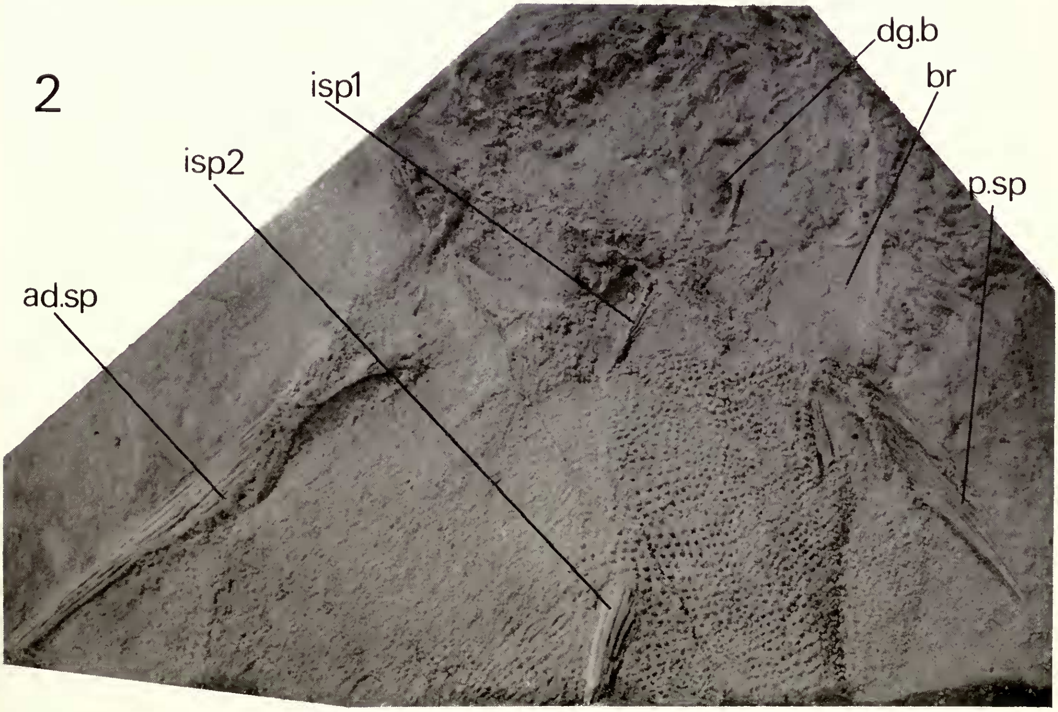


PLATE 14

Acanthodes bronni Agassiz

Lower Permian, Lebach, Germany. Shoulder-girdle and fin skeleton.

Fig. 1. Cast HU MB24. Photo: U. Samuelson.

Fig. 2. Cast BM P.49980, original HU MB14B. Photo: T. W. Parmenter.

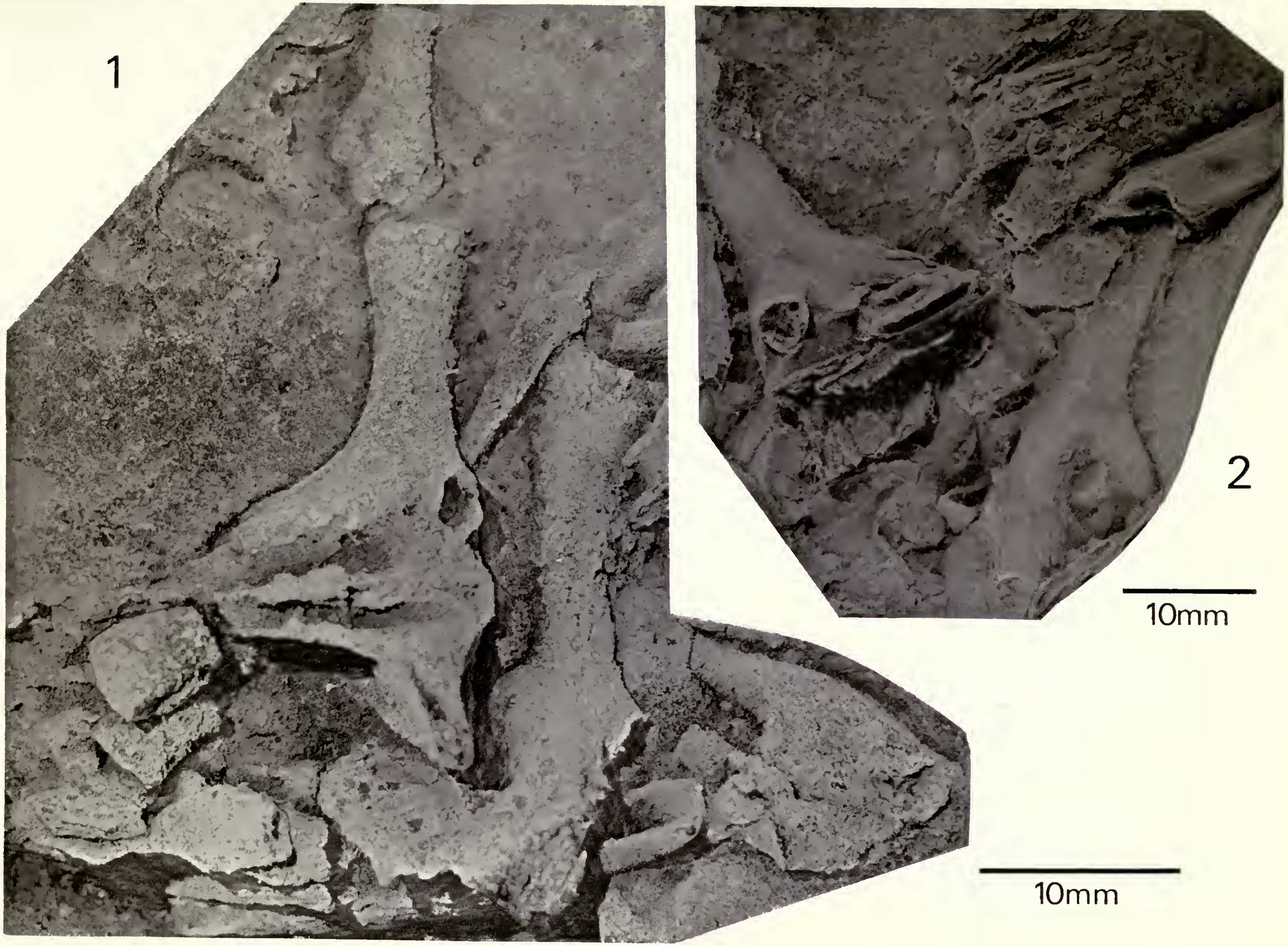

1
2
10mm
10mm

PLATE 15

Euthacanthus sp.

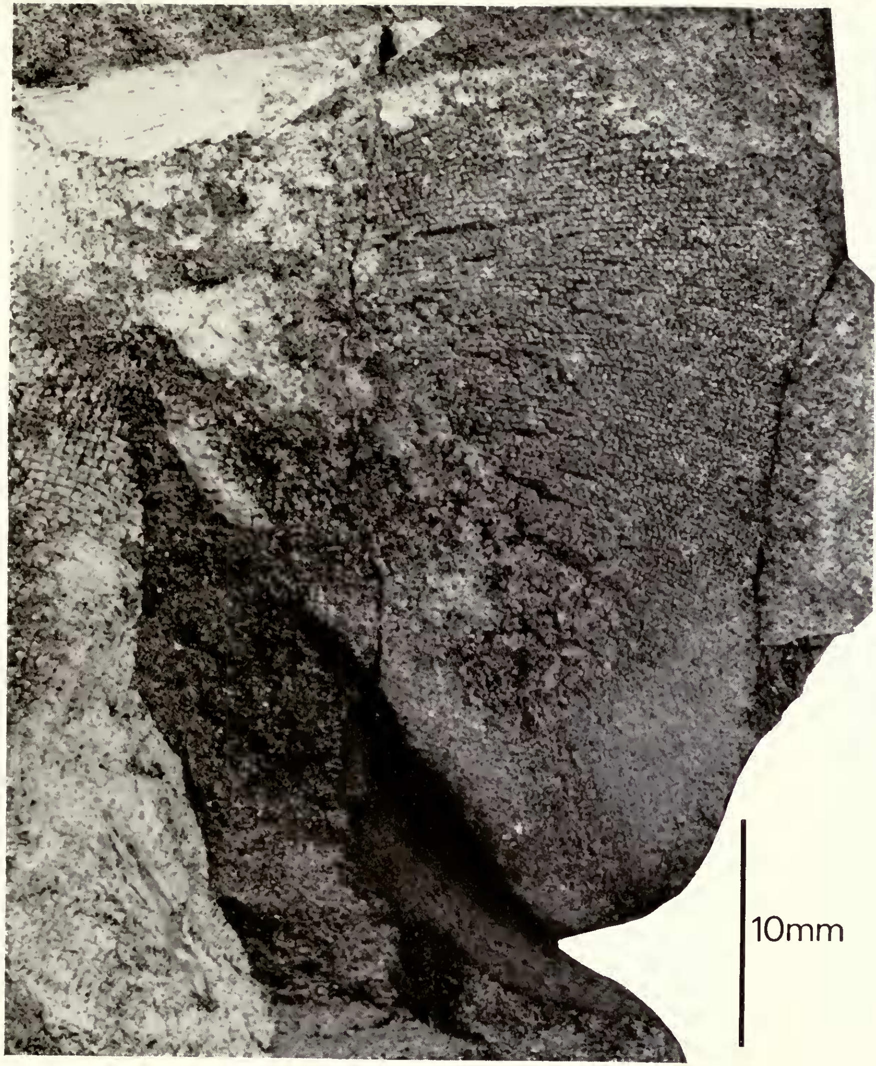
Fig. 1. Pectoral fin with lepidotrichia-like rows of scales. RSM 1971.38. Lower Old Red Sandstone, Angus (?), Scotland.

Cheiracanthus sp.

Fig. 2. Scapula and procoracoid. RSM 1868.19.18. Middle Old Red Sandstone, Tynet Burn, Banffshire, Scotland.

Photos: R. C. M. Thomson.

1



2

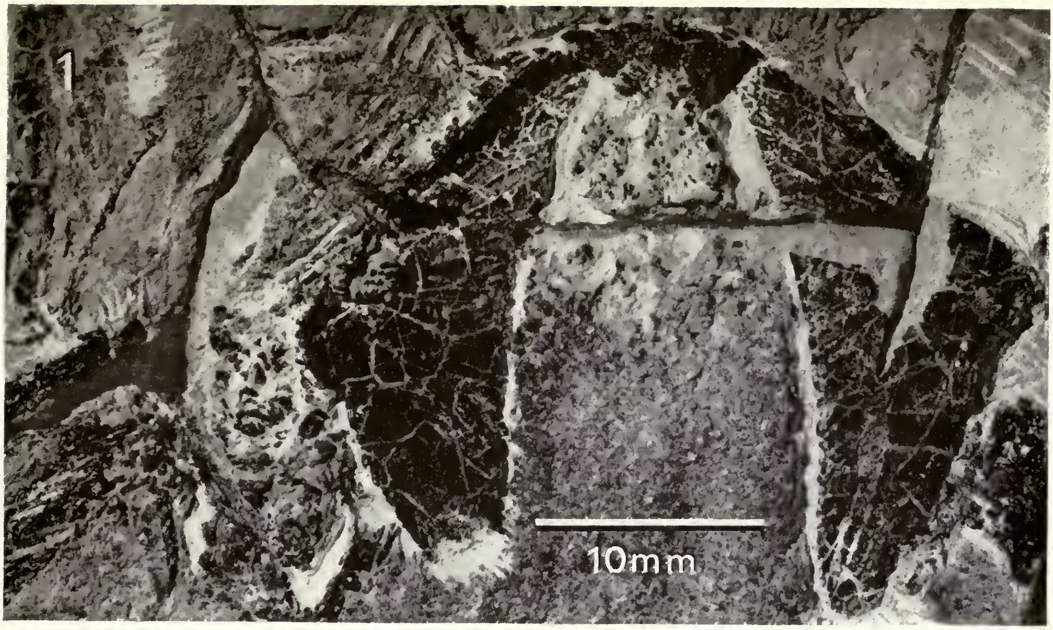
PLATE 16

Parexus falcatus Powrie

Fig. 1. Dermal shoulder-girdle in ventral view. RSM 1891.92.207. Arbuthnott Group, Dundee Formation, Lower Old Red Sandstone, Turin Hill, Angus, Scotland. Photo: R. C. M. Thomson.

Climatius reticulatus Agassiz

Fig. 2. Dermal shoulder-girdle, right side, in ventral view. BM P.6964b. Horizon and locality as for fig. 1. Photo: T. W. Parmenter.


1
10mm

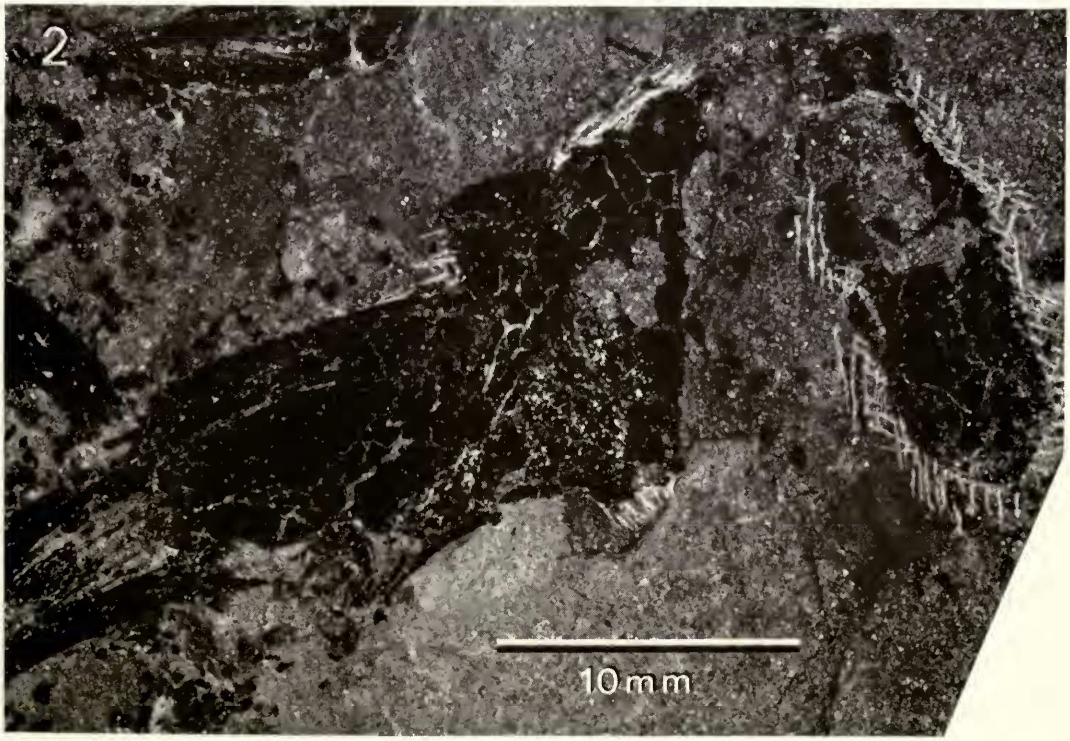

2
10mm

PLATE 17

Sabrinacanthus gen. nov. **arcuatus** (Agassiz)

Ditton Series, Lower Old Red Sandstone, Nass House, Lydney, Gloucester, England.

FIG. 1. Cast of BM P.53122a. Scapulocoracoid in mesial view. Use Text-fig. 29D as key-diagram.

FIG. 2. Cast of BM P.53121b. Shoulder-girdle and left pectoral spine in ventral view.

FIG. 3. Cast of BM P.53121a. Counterpart of specimen shown in fig. 2.

Photos: T. W. Parmenter.

1

2

3

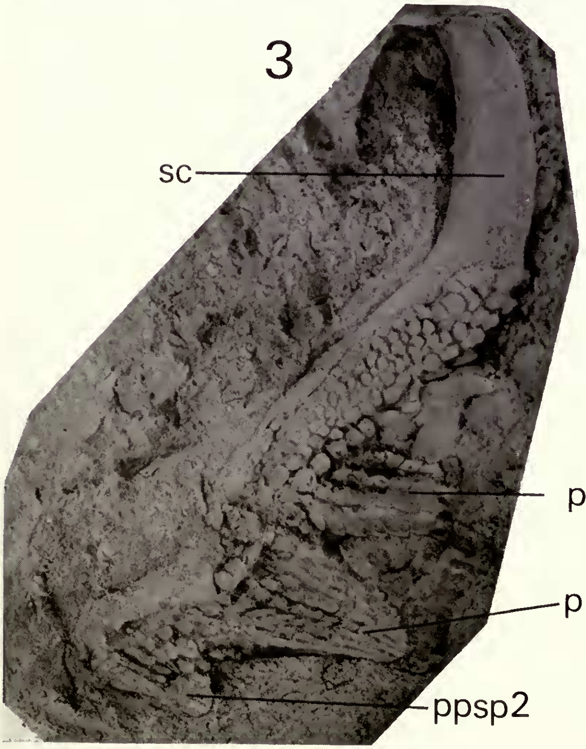


PLATE 18

Erriwacanthus manbrookensis sp. nov.

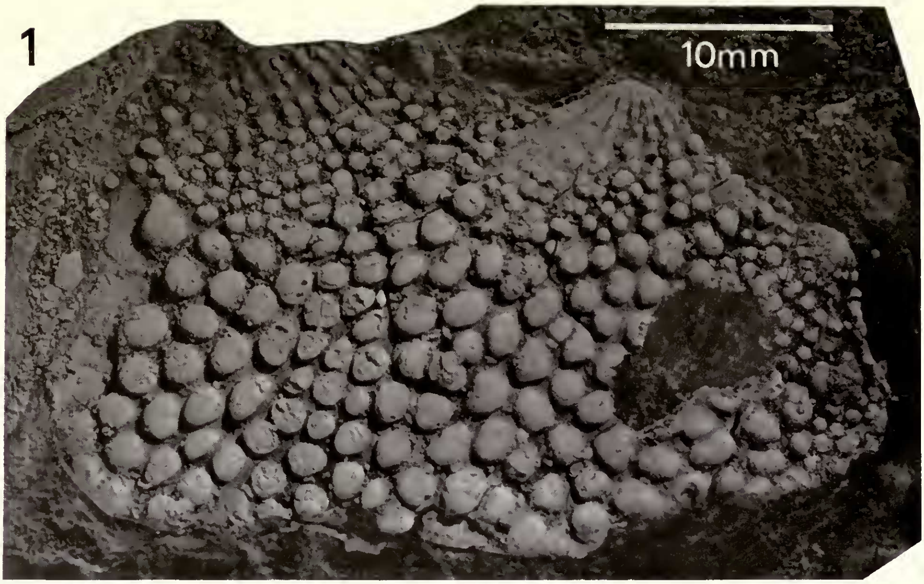
FIG. 1. Ascending left pinnal lamina with prepectoral spines. The keyhole-shaped foramen is due to post-mortem damage. BM P.48984. Downton Series, Red Marl Group, Man Brook 7, Shatterford, Trimpley, Worcestershire.

Euthacanthus macnicoli Powrie

FIG. 2. Right shoulder-girdle. Cast of GSM 88923. Arbuthnott Group, Dundee Formation, Lower Old Red Sandstone, Turin Hill, Angus, Scotland.

Photos: T. W. Parmenter.

1



2

PLATE 19

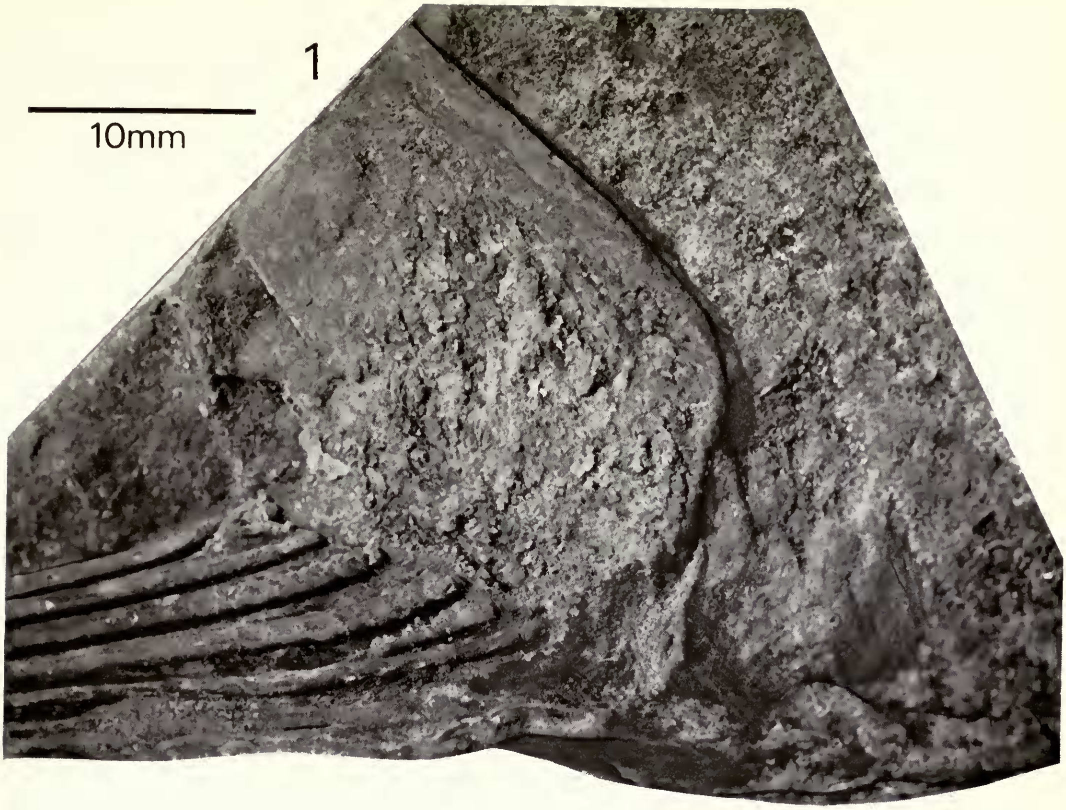
Ptomacanthus sp. indet 1

FIG. 1. Cast of BM P.17290 in lateral view. Ditton Series, Castle Mattock quarry, Cladock, Herefordshire, England.

Parexus recurvus Agassiz

FIG. 2. Dermal shoulder-girdle, right side, in lateral view. RSM 1956.14.14. Arbuthnott Group, Dundee Formation, Lower Old Red Sandstone, Turin Hill, Angus, Scotland.

Photos: R. C. M. Thomson.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10mm

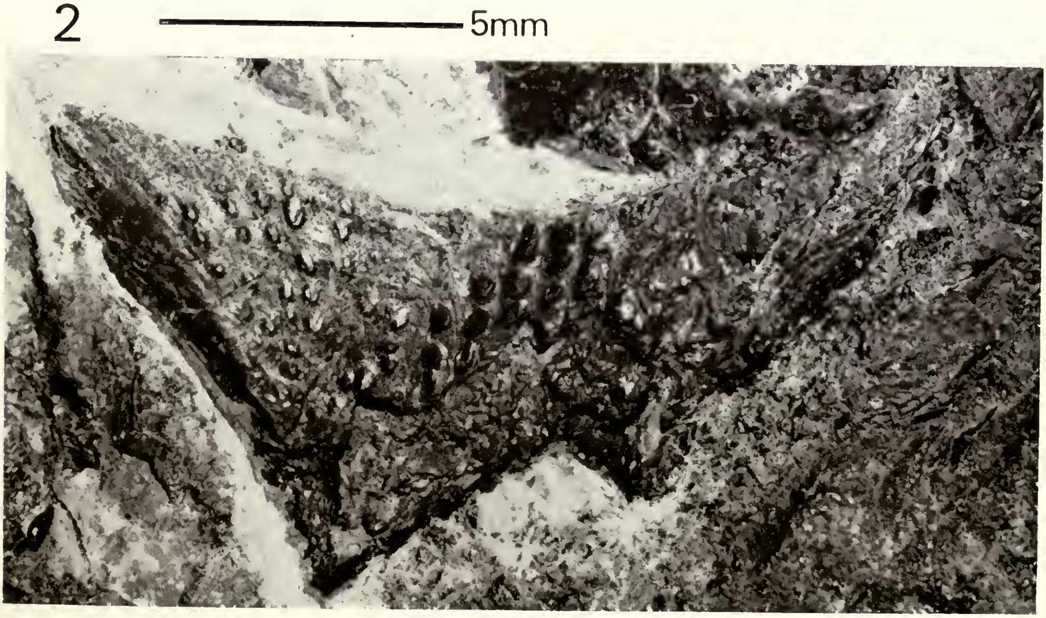
2
5mm

PLATE 20

Ptomacanthus sp. indet 2

Fig. 1. Shoulder-girdle in lateral view. SMNH P.6841. Dittonian, Zalerzychi, Ukranian SSR.

Cheiracanthus murchisoni Agassiz

Fig. 2. Pectoral fin with 'ceratotrichia'. BM P.9772. Middle Old Red Sandstone, Tynet Burn, Banffshire, Scotland.

Photos: Tordis Junker.

1

2

PLATE 21

Gyracanthus formosus Agassiz

Paired prepectoral spine and associated plate. BM P.45864. Low Main Seam, Upper Carboniferous, Newsham, Northumberland, England.

FIG. 1. Ventral view.

FIG. 2. Dorsal view.

Photos: Tordis Junker.


1
10mm
2